CHAPTER 2

Seasonal occurrence

of

parasites of free-living mammals

Introduction

The seasonal occurrence of parasites of wild mammals is presented and discussed here. Much of it is my own work, where I did the helminth identifications. Associates are E. Young (for whom I did the helminth identifications), M. Baker (where I also did the helminth identifications), U. Zieger (for whom I identified the helminths), K.J. Fellis and N.J. Negovetich (who used the data from the surveys of Boomker and Horak in the Kruger National Park, and whose manuscripts I edited), W.A. Taylor (for whom I identified the worms and was an advisor for his PhD thesis), M.B. Ellis (whose helminth identifications I confirmed or rejected, and extensively edited the manuscript), and then the numerous papers that I.G. Horak and I published as collaborators. He would often do the helminths, while I would check his identifications (!), or he would merely give me the helminths to identify, while I would give him the ectoparasites to identify from my own surveys.

These surveys gave extensive information on the fluctuation of helminth populations in the various species that they were done on. It emphasized the differences between the helminth intensities of browsers, grazers and intermediate feeders. It also provided information on the different helminth species in the various hosts. For example, *Haemonchus vegliai* is the main abomasal species in kudus, whereas *Haemonchus krugeri* and *Longistrongylus sabie* are the main ones in impalas. The publications are listed in chronological order.

HELMINTH PARASITES (P 133)

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HELMINTH COMMUNITIES (P 331)

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HELMINTH PARASITES

Onderstepoort J. vet. Res. 40 (2), 69–70 (1973)

HELMINTHS FROM THE MOUNTAIN REEDBUCK, *REDUNCA FULVORUFULA* (AFZELIUS, 1815)

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ABSTRACT

BAKER, MAUREEN K. & BOOMKER, J. Helminths from the mountain reedbuck, *Redunca fulvorufula* (Afzelius, 1815). *Onderstepoort J. vet. Res.* 40 (2), 69–70 (1973).

Helminth parasites recovered from the mountain reedbuck in the Loskop Dam Nature Reserve and the Mountain Zebra National Park are recorded. The following species are new host records: *Moniezia expansa, Cooperia hungi, C. oncophora, C. pectinata, C. yoshidai, Gongylonema* sp, *Haemonchus krugeri, Impalaia tuberculata, Nematodirus spathiger, Oesophagostomum columbianum, Skrjabinema* sp.

INTRODUCTION

Although the helminth fauna of many African antelopes is relatively well known (Ortlepp, 1961; Round, 1968), there is a dearth of data on the rarer species such as the mountain reedbuck, *Redunca fulvorufula* (Afzelius, 1815). Round (1968) lists six helminths from this antelope, viz. *Paramphistomum bothriophoron* (Braun, 1892), *Paramphistomum cervi* (Zeder, 1790), *Cysticercus tenuicollis* Rudolphi, 1810, *Haemonchus contortus* (Rudolphi, 1803), *Setaria boulengeri* Thwaite, 1927, and *Setaria hornbyi* Boulenger, 1921.

During 1969 and 1970 this antelope was the subject of an ecological study in the Loskop Dam Nature Reserve in the Transvaal. This necessitated the regular culling of a number of animals and special efforts were made to collect the helminths from them. During 1971 helminths were also recovered from mountain reedbuck in the Mountain Zebra National Park at Cradock, in the Cape Province.

MATERIALS AND METHODS

In the Loskop Dam Nature Reserve, helminths were recovered from the rumen, abdominal cavity and skeletal muscles of 42 reedbuck. Intestinal helminths were recovered from 11 of these animals, but it was possible to do total collections in four instances only.

In four reedbuck from the Mountain Zebra National Park the abdominal cavity and the intestinal tract were examined for helminths.

The descriptions of Ransom (1911), Mönnig (1931; 1932; 1939) and Travassos (1937) were used to identify the *Cooperia* spp.; Ransom (1911) and Ortlepp (1964) for *Haemonchus* spp.; Mönnig (1924) for the *Impalaia* sp.; Becklund & Walker (1967) for the *Nematodirus* sp.; Ransom (1911) for the *Oesophagostomum* sp. and Yeh (1959) for the *Setaria* sp.

RESULTS AND COMMENTS

The species of helminths recovered are listed in Table 1.

Conical flukes, *Paramphistomum* sp., were present in the rumen of 14 animals. Cysticerci were recovered from the skeletal muscles of 10 reedbuck. The rostellar hooks of these cysticerci resembled those of *Taenia crocutae* Mettrick & Beverley-Burton, 1961, in their number, size and shape (Verster, 1969).

Only one female of a *Gongylonema* sp. was recovered and it could not be identified specifically, nor could the five females and one severely damaged male of a *Skrjabinema* sp.

The apparent predominance of *S. boulengeri*, found in 42 of the 46 hosts, undoubtedly reflects the conditions under which the parasites were collected, i.e. in the field and often in poor light. Since *S. boulengeri* is a large nematode occurring in the abdominal cavity, it is more easily seen than the other smaller nematodes, particularly those inhabiting the intestine.

TABLE 1 Helminths recovered from the mountain reedbuck

Parasite	No. of Animals Infested
Loskop Dam Nature Reserve	
Paramphistomum sp.	14
Cysticercus sp.	10
*Cooperia hungi** Mönnig, 1931	3
*Cooperia oncophora** (Railliet, 1898)	1
*Cooperia pectinata** Ransom, 1907	1
*Cooperia punctata** Linstow, 1907	1
*Cooperia yoshidai** Mönnig, 1939	4
Cooperia sp.	2
*Gongylonema** sp.	1
Haemonchus contortus (Rudolphi, 1803)	7
*Haemonchus krugeri** Ortlepp, 1964	1
*Impalaia tuberculata** Mönnig, 1923	3
*Oesophagostomum columbianum** Curtice, 1890	2
Setaria boulengeri Thwaite, 1927	38
*Skrjabinema** sp.	4
Mountain Zebra National Park	
*Moniezia expansa** (Rudolphi, 1810)	1
Haemonchus sp.	1
*Nematodirus spathiger** (Railliet, 1896)	4
Setaria boulengeri Thwaite, 1927	4

*New host record.

Cooperia spp. occurred in eight animals and were the predominant nematodes in the total collections from the small intestine. The small intestine of one animal contained 1 107 specimens representing the species *C. hungi, C. oncophora, C. pectinata* and *C. yoshidai*. In this animal *C. yoshidai* outnumbered the other *Cooperia* spp. in a ratio of six to one. A second animal harboured *C. hungi, C. oncophora* and *C. yoshidai*, while a third had *C. hungi* and *C. yoshidai*. In two instances, only females were present and a specific diagnosis was therefore impossible.

H. contortus was recovered from seven animals. One reedbuck was simultaneously infested with *H. krugeri* and *H. contortus* in a ratio of one to 25. Female *Haemonchus* spp. only were present in one animal examined in the Mountain Zebra National Park.

N. spathiger was present in all the animals examined in the Mountain Zebra National Park but did not occur in those from the Loskop Dam Nature Reserve. Its absence from the latter animals is not unexpected as it has not yet been recorded from the Transvaal. It is, however, of major importance in sheep in the Karoo (Viljoen, 1964; 1968).

Received 8 May 1973 - Editor

Acknowledgements

The authors wish to express their sincere gratitude to Mr L. Irby of the Texas A & M University, U.S.A., who collected the parasites in the Loskop Dam Nature Reserve; Dr E. Young, State Veterinarian, Skukuza, who collected the parasites in the Mountain Zebra National Park and Dr Anna Verster, whose constant interest and valuable comments made this publication possible.

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Onderstepoort J. vet. Res., 51, 253–256 (1984)

THE HELMINTHS OF VARIOUS ANTELOPE SPECIES FROM NATAL

J. BOOMKER[1], M. E. KEEP[2], J. R. FLAMAND[3] and I. G. HORAK[4]

ABSTRACT

BOOMKER, J., KEEP, M. E., FLAMAND, J. R. & HORAK, I. G., 1984. The helminths of various antelope species from Natal. *Onderstepoort Journal of Veterinary Research*, 51, 253–256 (1984).

Helminth parasites were collected from 2 bushbuck, *Tragelaphus scriptus*, 2 red duiker, *Cephalophus natalensis*, 1 oribi, *Ourebia ourebi*, and 4 reedbuck, *Redunca arundinum*, that died or were culled in various parts of Natal. One trematode genus, 1 cestode genus and 12 nematode species were recovered. *Haemonchus contortus, Ostertagia harrisi, Trichostrongylus capricola, Trichostrongylus vitrinus, Cooperia rotundispiculum* and *Setaria scalprum* are new parasite records for the red duiker. *Trichostrongylus colubriformis* is a new parasite record for the oribi and *Longistrongylus schrenki, Trichostrongylus falculatus, Trichostrongylus colubriformis* and *Dictyocaulus viviparus* are recorded from the reedbuck for the first time. An unidentified paramphistome was also recovered from the reedbuck.

INTRODUCTION

The helminths of antelope occurring in and around the Natal game reserves have received little attention in the past. Such parasites as are known have been collected incidentally. The only records of the helminth burdens in bushbuck, *Tragelaphus scriptus*, oribi, *Ourebia ourebi*, common reedbuck, *Redunca arundinum*, and red duiker, *Cephalophus natalensis*, from this province of South Africa are provided by Le Roux (1930) and Keep (1983).

The habitat and food preferences of bushbuck and oribi in the Transvaal have been briefly described by Boomker, Horak & De Vos (1984). Both antelope are browsers, feeding on a large variety of plants.

The red duiker is a small antelope that is restricted to forested areas (Rautenbach, 1982). Very little is known about this animal, but Pienaar (1963) and Heinichen (1972) state that it is a delicate browser. Heinichen (1972) found it to be a nocturnal species, occurring singly or in pairs.

Reedbuck are medium-sized antelope that occur in well-grassed flatlands or rolling hills close to permanent water (Dorst & Dandelot, 1972; Rautenbach, 1982). Jungius (1971) and Venter (1979) discussed their ecology and food plant references and concluded that they are grazers, feeding for a large part on grasses unpalatable to other antelope.

The helminths recovered from these antelope are listed by Round (1968). Boomker *et al.* (1984) updated the list of parasites from bushbuck and oribi in the Transvaal, and Keep (1983) updated that of the helminths from the larger indigenous mammal species in Natal.

MATERIALS AND METHODS

Two male bushbuck and 2 red duiker males were shot in March 1983 at Charters Creek (28°14′S; 32°25′E) on the western shores of Lake St Lucia. Their gastro-intestinal parasites were collected as described by Reinecke (1973). The hearts, lungs and livers were processed for parasite recovery as described by Horak (1978a).

The parasites of a single male oribi, which died on a farm near Pietermaritzburg (29°58′S; 29°52′E) in September 1982, were collected.

Four male reedbuck were collected at different localities in Natal. Two were from near the Himeville Nature Reserve (29°44′S; 29°32′E) and were shot in August and December 1982 respectively. Another was obtained at Midmar Dam (29°30′S; 30°9′E) in October 1982, and the 4th was killed by a vehicle near Estcourt (28°58′S; 29°52′E) in December 1982.

The parasites of the rumen, the abomasal contents and digests, the small and large intestinal contents, the lungs and the abdominal cavity of 1 of the reedbuck from Himeville (No. 1) and the 1 from Midmar Dam (No. 2) were collected. Only the abomasal and small intestinal contents of the second animal from Himeville (No. 4) and the abomasal contents of the animal from Estcourt (No. 3) were available for examination. None of their hearts and livers were processed for parasites.

Separate aliquots representing 1/10th of the volume of the ingesta of the abomasum, small and large intestines of the 2 red duikers were examined for parasites. Two aliquots, each representing 1/50th of the volume of the gastro-intestinal ingesta of the bushbuck, were examined. Total parasite counts were made on the ruminal, abomasal and intestinal contents of each of the reedbuck and the oribi.

RESULTS

The helminths recovered from the bushbuck and the red duikers are listed in Table 1. Four nematode species and the larvae of a cestode were recovered from the bushbuck, and 6 nematode species from the red duikers. All the parasites found in the red duikers are new records for this antelope in South Africa.

The oribi harboured the following parasites: *Trichostrongylus falculatus*, 61 males; *Trichostrongylus colubriformis*, 6 males; *Trichostrongylus* spp., 52 females; *Cooperia yoshidai*, 9 males and 8 females. A total of 136 worms were recovered of which *T. colubriformis* represents a new parasite record.

The helminths from the reedbuck are listed in Table 2. One trematode genus and 8 nematode species were recovered, the paramphistome, *Longistrongylus schrenki, T. falculatus, T. colubriformis* and *Dictyocaulus viviparus being new parasite records*.

DISCUSSION

When compared with the numbers of species recovered and the size of the worm burdens of bushbuck from the Kruger National Park (KNP), as reported by Boomker *et al.* (1984), the 2 bushbuck from Charters Creek, Natal, had fewer species and smaller burdens. One possible explanation is that relatively few antelope species are found at Charters Creek, and that those that do occur there, such as greater kudu, nyala, bushbuck, red, blue and grey duikers, are almost exclusively browsers that usually carry few worms. *Ostertagia harrisi, Setaria africana* and *Taenia* spp. larvae were found in bushbuck from both localities, but *Gongylonema* sp. occurred in 1 bushbuck from Charters Creek only.

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Received 2 August 1984—Editor

TABLE 1 The helminth burdens of bushbuck and red duikers from Charters Creek, Lake St Lucia

Host, age and sex	*Haemonchus contortus*		*Ostertagia harrisi*			*Trichostrongylus* spp.	*Trichostrongylus capricola*	*Trichostrongylus vitrinus*	*Cooperia rotundis-piculum*		*Paracooperia devossi*			*Gongylonema* sp.		*Setaria scalprum*	*Setaria africana*		*Taenia* spp. larvae	Total worm burden
	♀	♂	L_4	♀	♂	♀	♂	♂	♀	♂	L_4	♀	♂	♀	♂	♀	♀	♂		
Bushbuck:																				
Prime adult ♂	0	0	0	24	14	0	0	0	0	0	0	1	111	2	1	0	2	1	1	157
Old ♂	0	0	0	60	47	0	0	0	0	0	30	11	11	0	0	0	2	2	1	164
Red Duiker:																				
Young adult ♂	0	0	2	2	0	267	165	0	0	0	0	0	0	0	0	0	0	0	0	436
Old ♂	10	10	1	3	2	2 212	1 075	153	600	461	0	0	0	0	0	1	0	0	0	4 528

L_4 = 4th stage larvae

TABLE 2 The helminth burdens of common reedbuck from various localities in Natal

Date and locality	No.	Age and sex	Paramphistomes	*Haemonchus contortus*			*Longistrongylus schrenki*			*Cooperia yoshidai*			*Trichostrongylus* spp.	*Trichostrongylus falculatus*	*Trichostrongylus colubriformis*	*Dictyocaulus viviparus*			*Setaria* spp.	*Bunostomum* sp.	Total worm burden
			A	L_4	♀	♂	L_4	♀	♂	L_4	♀	♂	♀	♂	♂	L_4	♀	♂	♀	♀	
Himeville:																					
Aug 1982	1	Adult ♂	30	0	0	2	0	4	5	2	103	83	0	0	0	6	8	6	6	0	255
Dec 1982	4	Adult ♂	5	4	25	68	8	18	4	0	752	672	0	0	0	0	2	1	9	29	1 597
Midmar Dam:																					
Oct 1982	2*	Adult ♂	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Estcourt:																					
Dec 1982	3**	Subadult ♂	0	0	18	13	0	53	31	0	643	665	159	23	13	0	0	0	0	0	1 618

A = Adults
L_4 = 4th stage larvae
* = only abomasal parasites collected
** = only abomasal and small intestinal parasites collected

The finding of *Paracooperia devossi* in the Natal bushbuck supports the argument of Boomker & Kingsley (1984) that this parasite has only recently become a parasite of bushbuck. This parasite had not previously been found in any bushbuck from the various Natal game reserves (Keep, 1983), and so far it appears to be confined to the eastern parts of the country.

The helminths recovered from the red duikers are interesting. *Haemonchus contortus* is a cosmopolitan parasite of artiodactylids (Gibbons, 1979), and in South Africa it is usually associated with domestic animals or with antelope in contact with domestic animals (Boomker, unpublished data, 1981). Although currently there are no domestic ruminants at Charters Creek, they were there prior to its proclamation as part of the St Lucia Nature Reserve (Pringle, 1982), and their nematodes were possibly passed on to the antelope during that time.

The 2 *Trichostrongylus* spp. that were recovered were identified as *Trichostrongylus capricola* and *Trichostrongylus vitrinus,* although neither conforms exactly to its description as given by Ransom (1911) and Looss (1905). *T. capricola* from the red duikers had spicules 0,092–0,120 mm long as opposed to 0,130–0,149 mm recorded by Ransom (1911), and 0,114–0,149 mm recorded by Levine (1980). *T. vitrinus* had spicules 0,120–0,159 mm long as opposed to 0,160–0,170 mm given by Looss (1905) and 0,149–0,176 mm given by Levine (1980). The shorter spicule lengths may be due to the host's reaction stimulated by prior infestations, as described by Keith (1967), for *Cooperia pectinata.* Specimens from Europe of both *T. capricola* and *T. vitrinus* from sheep and goats were examined, and the length of their spicules found to be within the ranges given by Levine (1980). The membraneous alae surrounding the spicules, however, were not as well developed as those of the worms from the red duikers. Futhermore, Levine (1980) states that *T. capricola* occurs in the small intestine and abomasum of its hosts and *T. vitrinus* in the duodenum and rarely in the abomasum. Both species, however, occurred predominantly in the abomasa of the red duikers. *T. capricola* has not been recorded before from South African artiodactylids, either free-living or domesticated, but *T. vitrinus* has been found in sheep in the south-western Cape Province (Muller, 1968). Because both the dorsal ray and the spicules of the *Trichostrongylus* spp. from the red duiker were similar to those of *T. capricola* and *T. vitrinus,* they are identified as such, although closer scrutiny may prove them to be new species.

As yet, *O. harrisi* has been found only in bushbuck (Round, 1968; Boomker *et al.*, 1984), from which it was originally described (Le Roux, 1930). Its presence in the red duikers is probably due to the close association of these antelope and bushbuck at Charters Creek, as well as their similar habitat preferences.

The parasites of the oribi from Pietermaritzburg are somewhat similar to those of the oribi from the KNP (Boomker *et al.*, 1984). *Impalaia tuberculata, Cooperia fuelleborni* and *O. columbianum,* however, were not present in the Natal oribi and *T. instabilis* was replaced by *T. colubriformis*. From this and other surveys of the helminth parasites of antelope it appears that *I. tuberculata* and *T. instabilis* favour the drier parts of the country such as the Transvaal Bushveld and Lowveld.

Keep (1983) lists the helminths recovered from the reedbuck, but since no references to previous studies on their burdens in South Africa could be found, no comparisons could be made with the results of this investigation. *H. contortus*, *T. falculatus* and *T. colubriformis* are common parasites of ruminants, both domestic (Viljoen, 1964, 1969; Muller, 1968) and free-living (Horak, 1978a, b).

C. yoshidai was originally described from the reedbuck (Mönnig, 1939), but it has subsequently also been recorded from mountain reedbuck (Baker & Boomker, 1973), blesbok (Evans, 1978; Horak, Brown, Boomker, De Vos & Van Zyl, 1982; Keep, 1983) and oribi (Boomker *et al.*, 1984). *C. yoshidai* appears to be well adapted to all the hosts in which it has been found.

D. viviparus occurs on isolated farms (Reinecke, 1983) and was recovered only from the 2 reedbuck shot at Himeville. This village is situated in an area that forms part of the eastern watershed where the summers are moderate and the winters cold. The conditions are favourable for the survival of the free-living stages, which are sensitive to heat and desiccation, but are resistant to cold (Oakley, 1979).

Small numbers of *L. schrenki* were recovered from 3 out of the 4 reedbuck. It has not been reported from South African ruminants since its description (Ortlepp, 1939), and it appears to be a rare parasite.

ACKNOWLEDGEMENTS

We should like to thank the Director, Natal Parks Board, for placing the animals at our disposal and for providing the facilities to process them for parasite recovery. The assistance of Messrs Tony Tomkinson, warden, and Wynand Kanfer, a ranger at Charters Creek, and of Mrs Shirley Kingsley with the processing of the animals is gratefully acknowledged.

This study was partly funded by the Council for Scientific and Industrial Research and the University of Pretoria.

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Printed by the Government Printer, Private Bag X85, Pretoria, 0001

Onderstepoort J. vet. Res., 53, 93–102 (1986)

THE HELMINTH PARASITES OF VARIOUS ARTIODACTYLIDS FROM SOME SOUTH AFRICAN NATURE RESERVES

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ABSTRACT

BOOMKER, J., HORAK, I. G. and DE VOS, V., 1986. The helminth parasites of various artiodactylids from some South African nature reserves. *Onderstepoort Journal of Veterinary Research* 53, 93–102 (1986)

The helminth species composition and helminth burdens of 4 grey duikers, 12 bushbuck, 2 nyala, 2 giraffe, a steenbok, an oribi, a waterbuck and a tsessebe from the Kruger National Park (KNP); of a steenbok and a greater kudu from the farm Riekerts Laager, Transvaal; of a single blue duiker from the Tsitsikama Forest National Park, and of a blue wildebeest, a red hartebeest, a gemsbok and 2 springbok from the Kalahari Gemsbok National Park (KGNP) were collected, counted and identified

New parasite records are: *Agriostomum equidentatum* from the gemsbok, *Cooperia neitzi* from the bushbuck, *Cooperia* sp. from the gemsbok and the red hartebeest, *Cooperia yoshidai* from the waterbuck and the tsessebe, *Dictyocaulus viviparus* from the bushbuck, *Haemonchus bedfordi* from the waterbuck, *Haemonchus contortus* from the gemsbok, *Haemonchus krugeri* from the steenbok from the KNP, *Impalaia nudicollis* from the gemsbok and the red hartebeest, *Impalaia tuberculata* from the oribi and the waterbuck, *Impalaia* spp. from the kudu, *Longistrongylus meyeri* from the steenbok from Riekerts Laager and the gemsbok, *Longistrongylus sabie* from the steenbok from the KNP, *Longistrongylus schrenki* from the tsessebe, *Parabronema* sp. from the tsessebe and the red hartebeest, *Paracooperia serrata* from the gemsbok and the steenbok from the KGNP, *Pneumostrongylus calcaratus* from the bushbuck, *Strongyloides* sp. from the gemsbok, *Trichostrongylus* sp. from the gemsbok, the red hartebeest and the steenbok from the KGNP, *Trichostrongylus axei* from the blue duiker, *Trichostrongylus falculatus* from the bushbuck and the oribi, *Trichostrongylus instabilis* from the bushbuck, the steenbok from the KNP and the oribi and *Trichostrongylus thomasi* from the grey duikers and tsessebe.

Host specificity of the parasites was not marked and crossinfestation was common. This was not true for the giraffe, since none of the helminths of these animals were found in the antelope and vice versa.

INTRODUCTION

Many artiodactylids in game reserves die annually from accidents or diseases or are culled for research or other purposes not necessarily related to parasitological surveys. By collecting the internal parasites of such animals, valuable information on the species composition of their helminths and their helminth burdens can be obtained. This is particularly true in the case of rare species such as blue duiker, *Cephalophus monticola,* or species that are not well represented in a particular game reserve, such as nyala, *Tragelaphus angasi,* in the Kruger National Park (KNP).

The helminths recorded in this paper were recovered from 4 grey duikers, *Sylvicapra grimmia,* 1 blue duiker, *C. monticola,* 12 bushbuck, *Tragelaphus scriptus,* 2 nyala, *T. angasi,* 1 kudu, *Tragelaphus strepsiceros,* 2 giraffe, *Giraffa camelopardalis,* 3 steenbok, *Raphicerus campestris,* 1 oribi, *Ourebia ourebi,* 1 waterbuck, *Kobus ellipsiprymnus,* 1 tsessebe, *Damaliscus lunatus,* 1 red hartebeest, *Alcelaphus buselaphus,* 1 blue wildebeest, *Connochaetes taurinus,* 1 gemsbok, *Oryx gazella* and 2 springbok, *Antidorcas marsupialis.*

MATERIALS AND METHODS

Animals

The animals and the localities at which they were collected are listed in Table 1.

Collection of parasites

Apart from the blue duiker, only the formalinized gastro-intestinal tract of which was available, the gastro-intestinal parasites were collected in the field using the methods described by Reinecke (1973) and formalinized. The hearts, lungs and livers were processed as described by Horak (1978b) and were also formalinized. Since the parasites of the animals from the Kalahari Gemsbok National Park (KGNP) were collected in the field, where no waterbaths were available, digests, hearts and lungs were placed in the sun or near an open fire to reach the desired temperature.

One aliquot representing 1/10th of the volume of the ingesta was made separately for each of the abomasa, small and large intestines of the 4 grey duikers, the blue duiker, the steenbok, the springbok and the oribi, while 2 aliquots, each representing 1/50th of the volume of the ingesta were made for each of the remaining animals. All the aliquots and digests as well as the heart, lung and liver washings were examined microscopically.

In cases where more than one species of a genus was present, the males were identified specifically but not the females. The 4th stage larvae were identified to the generic level only.

RESULTS

The total numbers of helminths recovered from the gastro-intestinal tracts of the various animals are listed in Tables 2 and 3.

Grey duikers (Table 2)

Two cestode and 9 nematode species, were collected. *Trichostrongylus thomasi* is a new parasite record for these antelope.

Blue duiker (Table 2)

Trichostrongylus axei was the only helminth recovered and is a new record for the blue duiker.

Bushbuck (Table 2)

One cestode and 13 nematode species were recovered of which *Cooperia neitzi, Trichostrongylus instabilis, Trichostrongylus falculatus, Dictyocaulus viviparus* and *Pneumostrongylus calcaratus* are new parasite records for these antelope.

Nyala (Table 2)

Both the nyala were males; the younger one (No. 1) did not harbour any worms. The older male (No. 2) had

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Received 11 November 1985—Editor

TABLE 1 The collection data for the various artiodactylids examined during this study

Species	Number	Date	Locality
Grey duiker	4	Feb. 80–Jan. 81	Malelane, Kruger National Park; 25°28'S; 31°31'E
Blue duiker	1	Oct. 76	Tsitsikama Forest National Park, Cape Province; 33°54'–33°57'S; 23°51'–23°56'E
Nyala	2	Oct. 81	Pafuri, Kruger National Park; 22°26'S; 31°10'E
Bushbuck	3	Oct. 81	Pafuri, Kruger National Park; 22°26'S; 31°10'E
Bushbuck	9	Oct. 79–Nov. 82	Skukuza, Kruger National Park; 24°58'S; 31°35'E
Giraffe	2	July 80	Lower Sabie, Kruger National Park; 25°07'S; 31°50'E
Steenbok	1	Nov. 79	Riekerts Laager, Transvaal; 24°30'S; 28°29'E
Steenbok	1	Oct. 82	Malelane, Kruger National Park; 25°28'S; 31°31'E
Steenbok	1	Oct. 84	Kalahari Gemsbok National Park; Approx. 24°30'–25°47'S; 20°–20°52'E
Oribi	1	July 79	Pretoriuskop, Kruger National Park; 25°10'S; 31°16'E
Waterbuck	1	Feb. 83	Pretoriuskop, Kruger National Park; 25°10'S; 31°16'E
Tsessebe	1	June 83	Pretoriuskop, Kruger National Park; 25°10'S; 31°16'E
Kudu	1	Oct. 79	Riekerts Laager, Transvaal; 24°30'S; 28°29'E
Red Hartebeest	1	Oct. 84	Kalahari Gemsbok National Park; Approx. 24°30'–25°47'S; 20°–20°52'E
Blue Wildebeest	1	Oct. 84	Kalahari Gemsbok National Park; Approx. 24°30'–25°47'S; 20°–20°52'E
Springbok	2	Oct. 84	Kalahari Gemsbok National Park; Approx. 24°30'–25°47'S; 20°–20°52'E
Gemsbok	1	Oct. 84	Kalahari Gemsbok National Park; Approx. 24°30'–25°47'S; 20°–20°52'E

1561 worms, none of which could be identified specifically. The *Cooperia* sp. that was recovered is closely related to *Cooperia rotundispiculum* but was not identical with it.

Giraffe (Table 2)

Only 2 species of worms, *Parabronema skrjabini* and *Monodontella giraffae* were recovered and both are known to occur in giraffe.

Kudu (Table 2)

Of the worms recovered from this animal *T. instabilis* and the *Impalaia* sp. females are new parasite records.

Steenbok (Table 3)

The paramphistome and the nematodes *Longistrongylus meyeri, Longistrongylus sabie, Haemonchus krugeri,* and *T. instabilis* are new parasite records.

Oribi (Table 3)

T. instabilis, T. falculatus and *Impalaia tuberculata* are new parasite records for this antelope.

Waterbuck (Table 3)

Haemonchus bedfordi, Cooperia yoshidai and *I. tuberculata* are new nematode records for waterbuck.

Tsessebe (Table 3)

C. yoshidai, Longistrongylus schrenki, T. instabilis, and *T. thomasi* appear to be new parasite records for this antelope.

Gemsbok (Table 3)

The following helminths appear to be new parasite records: *Haemonchus contortus, L. meyeri, Paracooperia serrata, Impalaia nudicollis, Strongyloides* and *Agriostomum equidentatum.*

Blue wildebeest (Table 3)

The only worms recovered were *H. bedfordi,* which is a known parasite of blue wildebeest.

Springbok (Table 3)

All the worms recovered in this survey are known to occur in springbok.

Red hartebeest (Table 3)

I. nudicollis and the *Parabronema* sp. are new parasite records.

DISCUSSION

Grey duiker

The mean helminth burdens and the species composition of the helminths recovered from the duikers from the KNP show some similarity to those of the duikers from the central Transvaal (Boomker, Du Plessis & Boomker, 1983). The mean total worm burden of the duikers from the KNP was 704 worms and that of the duikers from the central Transvaal was 870 (Boomker *et al.*, 1983). Certain parasites such as *T. axei* and *C. pectinata* are frequently found in domestic animals, and were also present in the duikers from the central Transvaal. In the KNP they were replaced by parasites such as *T. thomasi, C. hungi* and *C. neitzi,* which are found almost exclusively in wild antelope. This is attributed to the relatively closed ecosystem in the KNP, where domestic ruminants are as a rule not found and the fact that the duikers from Riekerts Laager had contact with sheep, goats and cattle.

Blue duiker

The only parasite thus far recorded from the blue duiker in South Africa is *Moniezia expansa* (Gough, 1908). No record of nematodes from this antelope from South Africa could be found in the literature and *T. axei* is thus the first and only one recorded.

Bushbuck

The helminth parasites of bushbuck from South Africa have been recorded by Veglia (1919), Mönnig (1928, 1931, 1933), Le Roux (1929, 1930a, b) and Ortlepp (1961). Gibbons & Khalil (1980) and Boomker & Kingsley (1984) found *Paracooperia tragelaphi* and *P. devossi* in East and South African bushbuck respectively. The present paper adds 3 trichostrongylids and 2 lungworms to the existing list.

The *Trichostrongylus* spp. could have been acquired from any of the antelope present in the KNP, since both *T. instabilis* and *T. falculatus* are the species most frequently encountered in the small intestine (Horak & Boomker, 1983, unpublished data).

The name *T. instabilis* for a *Trichostrongylus* sp. resembling *T. colubriformis* but with a short hook and a markedly bent spicular shaft, is retained here for reasons given by Horak (1980) and Boomker *et al.*, (1983).

The occurrence of *T. falculatus* is somewhat of an enigma. In the semi-arid areas, such as the Karoo it is the dominant *Trichostrongylus* spp. during the cold and dry winter months (Viljoen, 1964, 1969). In the summer rainfall areas, such as the Transvaal Highveld the worms are present in small numbers in winter (Horak & Louw, 1977; Horak, 1978a). *T. colubriformis* is the dominant worm in the non-seasonal rainfall areas where the winters are mild and frost seldom occurs (Muller, 1968). In the KNP, which falls within the summer rainfall area, the winters are also mild and this probably accounts for the small numbers of *T. falculatus* recovered.

The members of the genus occur in larger numbers during the cooler months of the year (Reinecke, 1964,

1983) but *T. falculatus* in the semi-arid areas may increase markedly in spring if preceded by good rains (Viljoen, 1964, 1969). Horak (1978c), however, recovered the largest numbers of *T. falculatus* from cattle in the northern Transvaal during December (summer). Horak & Louw (1978) found worms of this genus to be abundant in cattle on the Transvaal Highveld during June while few worms occurred from July–September. The largest *Trichostrongylus* spp. burdens in cattle in the northern Transvaal were present during December, and very few worms were present from July–October (Horak, 1978c). From the present data it is apparent that *Trichostrongylus* spp. are more abundant in the bushbuck at Skukuza from June–October, a finding which is contrary to that of Horak (1978c) from an area that has a similar climate as the KNP.

C. neitzi is commonly encountered in antelope in the KNP (Boomker, 1983, unpublished data) and its presence in bushbuck is therefore to be expected. The *Cooperia* sp. from 1 of the bushbuck and 1 of the nyala shot at Pafuri and 1 bushbuck from Skukuza is very closely related to *C. rotundispiculum*. However, its spicules are shorter and it has 18–20 longitudinal cuticular ridges as opposed to the 14 present in *C. rotundispiculum* (Gibbons, Lynda M., 1983, personal communication).

O. harrisi has been described from bushbuck (Le Roux, 1930a) and has recently also been found in red duiker (*Cephalophus natalensis*) (Boomker, Keep & Flamand, 1984) and nyala from Natal game reserves (Boomker, 1983, unpublished data).

H. vegliai appears to be the most common *Haemonchus* sp. occurring in the browsing antelope and its presence in bushbuck is therefore not unexpected. It was also found in the grey duikers in this study and in those from the central Transvaal (Boomker *et al.*, 1983) and has been found in kudu, both from the central Transvaal and the KNP (Boomker, 1983, unpublished data).

P. devossi seems to be a recently acquired parasite of bushbuck in the KNP as was discussed by Boomker & Kingsley (1984).

C. sagittus is a common parasite of the tragelaphine antelope (Round, 1968) and has also been found in Cape buffalo *Syncerus caffer* (McCully, Van Niekerk & Basson, 1967), domestic cattle in the Transvaal (Boomker, 1979, unpublished data) and nyala from Natal (Keep, 1971).

D. viviparus was recovered from 2 animals, a young female from Pafuri and an adult male from Skukuza. Both these animals were debilitated and we assume that the infestation became established because of their enfeebled state. The epidemiology of this parasite is largely unknown. Isolated foci occur in the mist belt of the Drakensberg, both in Natal and Transvaal, and it is rife on irrigated pastures. No explanation for its occurrence in bushbuck in the KNP can be offered, and it must be assumed that the bushbuck are abnormal hosts, since only 5th stage worms were recovered.

P. calcaratus was originally described from an impala (Mönnig, 1932), and a single male was found in 1 of the bushbuck only. This animal was collected in November, 1982, during a severe drought in the KNP when as many as 1 000 impala and numerous bushbuck, kudu and warthog congregated daily on the irrigated lawns of the golf course in the staff village at Skukuza. This lungworm probably originated from an impala. It has spicules slightly shorter than those recorded by Mönnig (1932), which is an indication that the bushbuck is probably an abnormal host.

Nyala

Keep (1971) recorded some of the parasites of nyala from some of the Natal game reserves, but nothing is known about those from the KNP. No comments can be made on the parasites collected during this survey, since both the nematode genera that were recovered could not be identified specifically.

Giraffe

Fertile hydatid cysts have been recorded from a giraffe in an Australian zoo (Kelly, Boray & Dixon, 1968) and Sachs, Gibbons & Lweno (1973) found 3 *Haemonchus* spp. in East African giraffe. Pester & Laurence (1974) found *Moniezia expansa* and Shoho & Sachs (1975) *Setaria labiatopapillosa* and *Pseudofilaria giraffae* in East and South African giraffe.

Ivashkin (1956) experimentally infested larvae of the fly *Haematobia titilans* (= *Lyperosia titilans*) with 1st stage larvae of *Parabronema skrjabini* obtained from camels. He found encysted 2nd stage larvae of this nematode in the pupae of the flies and concluded that the infested flies had to be eaten by the final host for the life cycle to be completed. Various species of *Haematobia* are present in South Africa and they are considered to be almost permanent parasites, leaving their hosts only to lay eggs (Howell, Walker & Neville, 1978). It is not known, however, whether the South African species of *Haematobia* are the intermediate hosts of *P. skrjabini*.

M. giraffae is a parasite of the bile ducts of giraffe and, being a hookworm, it is assumed that infestation occurred percutaneously.

Kudu

Condy (1972) recorded the helminths of kudu in Zimbabwe. The worms recovered from the kudu from Riekerts Laager were similar to those of the steenbok and grey duikers from the same locality (Boomker *et al.*, 1983). The *Trichostrongylus* spp. recovered from the steenbok and grey duikers, however, were not present in the kudu.

Steenbok

Virtually the same worms as those occurring in grey duikers from Riekerts Laager were found in the steenbok from the same locality, the only addition being *L. meyeri* and the *Skrjabinema* spp. (Boomker *et al.*, 1983). These worms could have been acquired from any of the antelope present on the farm or from sheep and goats outside the confines of the farm (Boomker *et al.*, 1983).

Similar parasites were recovered from the steenbok from the KNP, the difference being the presence of *H. krugeri*, *L. sabie* and *T. instabilis*, and the absence of *T. axei* and *L. meyeri*.

The larger helminth burden of the steenbok from the KNP is ascribed to the drought experienced at the time, which resulted in its emaciated and weakened condition, and hence greater susceptibility to infestation.

In addition to the *Skrjabinema* spp., which were found in the steenbok from all the localities, the steenbok from the KGNP harboured only *P. serrata* and a *Trichostrongylus* species. *P. serrata* was described from a springbok (Mönnig, 1931), which is the commonest antelope in the KGNP, and the steenbok could easily have acquired this parasite from the springbok. The as yet unnamed *Trichostrongylus* sp. has spicules that are dissimilar in appearance. They are 120–134 and 136–148 μm long and an earshaped, sclerotized protuberance is present on the shaft of the longer one.

Oribi, waterbuck and tsessebe

Although the antelope were shot at exactly the same locality, the rhino camp near Pretoriuskop in the KNP, there are distinct differences, both in halminth burdens

TABLE 2 The helminth burdens of the browsing artiodactylids from various localties

Species	Locality and date	No.	Age	Sex	*Parabronema skrjabini*			*Monodontella giraffae*		*Haemonchus vegliai*			*Ostertagia harrisi*			*Trichostrongylus* spp.	*Trichostrongylus axei*	*Trichostrongylus falculatus*	*Trichostrongylus instabilis*	*Trichostrongylus thomasi*	*Cooperia* spp.			*Cooperia punctata*
					L4	♀	♂	♀	♂	L4	♀	♂	L4	♀	♂	♀	♂	♂	♂	♂	L4	♀	♂	♂
Grey Duiker	*Malelane*																							
	February '80	10	Prime adult	♂	—	—	—	—	—	0	0	10	—	—	—	33	0	0	0	20	0	130	0	—
	May '80	12	Old adult	♂	—	—	—	—	—	0	12	4	—	—	—	48	0	0	0	22	0	3	0	—
	May '80	13	Prime adult	♀	—	—	—	—	—	53	0	0	—	—	—	0	0	0	0	1	0	13	0	—
	January '81	17	Young adult	♂	—	—	—	—	—	2	10	10	—	—	—	0	0	0	0	0	0	0	0	—
Blue Duiker	*Tsitsikama*																							
	October '76	—	Not known		—	—	—	—	—	—	—	—	—	—	—	200	210	—	—	—	—	—	—	—
Bushbuck	*Pafuri*																							
	October '81	1	Prime adult	♂	—	—	—	—	—	0	197	191	0	0	0	0	0	0	0	0	0	0	0	0
	October '81	2	Old	♂	—	—	—	—	—	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	October '81	3	Young adult*	♀	—	—	—	—	—	0	0	0	0	0	0	0	0	0	0	0	50	1 457	1 426	0
	Skukuza																							
	October '79	4	Adult	♀	—	—	—	—	—	0	75	75	0	125	75	0	0	0	0	0	0	0	0	0
	October '79	5	Very old	♂	—	—	—	—	—	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	August '80	6	Yearling	♂	—	—	—	—	—	0	0	0	0	125	50	25	0	0	0	0	0	0	0	0
	October '80	7	2 years	♂	—	—	—	—	—	0	0	0	0	0	0	0	0	0	0	0	0	75	0	0
	June '82	8	Juvenile	♂	—	—	—	—	—	50	50	26	1	36	5	545	0	2	132	0	0	25	0	0
	June '82	9	Juvenile	♂	—	—	—	—	—	0	25	0	380	1 738	1 097	126	0	100	0	0	25	0	0	0
	November '82	10	Adult	♀	—	—	—	—	—	0	25	75	0	0	0	25	0	0	50	0	0	150	0	0
	November '82	11	Adult	♂	—	—	—	—	—	0	0	0	0	203	154	360	0	165	0	0	0	0	0	0
	November '82	12	Adult*	♂	—	—	—	—	—	0	57	55	0	81	97	0	0	0	0	0	0	125	75	0
Nyala	*Pafuri*																							
	October '81	1	Adult	♂	—	—	—	—	—	0	0	0	0	0	0	—	—	—	—	—	0	0	0	—
	October '81	2	Adult	♂	—	—	—	—	—	0	25	0	0	0	0	—	—	—	—	—	4	1 052	480	—
Giraffe	*Lower Sabie*																							
	July '80	1	Adult	♂	404	7 372	11 050	186	145	0	0	0	—	—	—	—	—	—	—	—	0	0	—	0
	July '80	2	Adult	♂	0	823	1 213	215	370	0	0	0	—	—	—	—	—	—	—	—	0	0	—	0
Kudu	*Riekerts Laager*																							
	October '79	—	Old	♂	—	—	—	—	—	0	69	41	—	—	—	90	0	0	20	0	0	262	0	71

—	Not known to occur in this host		
A	Adult	+	Slight infestation
L4	4th stage larvae	++	Moderate infestation
5th	5th stage	Epg	Eggs per gram faeces
ND	Not done	*	Severely debilitated

TABLE 2 The helminth burdens of the browsing artiodactylids from various localties *(continued)*

Species	Locality and date	No.	Age	Sex	*Cooperia pectinata*	*Cooperia neitzi*	*Cooperia acutispiculum*	*Cooperia hungi*	*Impalaia* spp.		*Impalaia tuberculata*	*Paracooperia devossi*		*Oesophagostomum* spp.	*Gaigeria* spp.	*Longistrongylus* spp.	*Dictyocaulus viviparus*	*Pneumostrongylus calcaratus*	*Setaria* spp.	*Cordophilus sagittus*	Larvae of *Taenia* spp.	*Stilesia hepatica*	Total helminth burden	Epg
					♂	♂	♂	♂	L4	♀	♂	♀	♂	L4	♀	L4	5th	♂	A	A				
Grey Duiker	*Malelane*																							
	February '80	10	Prime adult	♂	0	30	50	0	0	490	340	—	—	10	0	0	—	—	1	—	0	+	1 114	100
	May '80	12	Old adult	♂	0	0	0	11	8	3	13	—	—	0	0	0	—	—	1	—	0	++	125	0
	May '80	13	Prime adult	♀	0	0	2	0	307	1	0	—	—	1	0	162	—	—	2	—	1	0	543	0
	January '81	17	Young adult	♂	0	0	0	0	388	282	352	—	—	0	0	0	—	—	0	—	8	0	1 052	300
Blue Duiker	*Tsitsikama*																							
	October '76	—	Not known		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	410	ND
Bushbuck	*Pafuri*																							
	October '81	1	Prime adult	♂	—	0	—	—	—	—	—	0	0	0	0	—	0	0	1	2	0	0	391	ND
	October '81	2	Old	♂	—	0	—	—	—	—	—	0	0	0	0	—	0	0	0	4	0	0	4	0
	October '81	3	Young adult*	♀	—	0	—	—	—	—	—	0	0	0	0	—	14	0	0	0	3	0	2 950	0
	Skukuza																							
	October '79	4	Adult	♀	—	0	—	—	—	—	—	0	0	0	0	—	0	0	0	0	0	0	350	ND
	October '79	5	Very old	♂	—	0	—	—	—	—	—	0	0	0	0	—	0	0	0	0	0	0	0	ND
	August '80	6	Yearling	♂	—	0	—	—	—	—	—	0	0	0	0	—	0	0	0	0	0	0	200	ND
	October '80	7	2 years	♂	—	25	—	—	—	—	—	0	0	0	0	—	0	0	0	0	0	0	100	ND
	June '82	8	Juvenile	♂	—	25	—	—	—	—	—	2	3	0	0	—	0	0	0	2	0	0	904	0
	June '82	9	Juvenile	♂	—	0	—	—	—	—	—	359	252	0	25	—	0	0	0	0	0	0	4 127	0
	November '82	10	Adult	♀	—	125	—	—	—	—	—	26	51	0	0	—	0	1	2	0	0	0	530	0
	November '82	11	Adult	♂	—	0	—	—	—	—	—	419	219	0	25	—	0	0	0	0	0	0	1 545	ND
	November '82	12	Adult*	♂	—	0	—	—	—	—	—	187	261	0	0	—	6	0	0	0	0	0	944	ND
Nyala	*Pafuri*																							
	October '81	1	Adult	♂	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	0	0	—	0	0
	October '81	2	Adult	♂	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	0	0	—	1 561	0
Giraffe	*Lower Sabie*																							
	July '80	1	Adult	♂	0	—	—	—	0	0	0	—	—	—	—	—	—	—	0	—	0	—	19 157	0
	July '80	2	Adult	♂	0	—	—	—	0	0	0	—	—	—	—	—	—	—	0	—	0	—	2 621	0
Kudu	*Riekerts Laager*																							
	October '79	—	Old	♂	20	0	0	0	0	10	0	0	0	0	0	—	—	—	0	0	0	—	583	ND

— Not known to occur in this host
A Adult
L4 4th stage larvae
5th 5th stage
ND Not done

+ Slight infestation
++ Moderate infestation
Epg Eggs per gram faeces
* Severely debilitated

TABLE 3 The helminth burdens of grazing antelope and of grazing and browsing antelope from various localities

Species	Locality and date	Age	Sex	*Paramphistomes*	*Haemonchus* spp.		*Haemonchus bedfordi*	*Haemonchus contortus*	*Haemonchus krugeri*	*Trichostrongylus* spp.			*Trichostrongylus axei*	*Trichostrongylus falculatus*	*Trichostrongylus instabilis*	*Trichostrongylus thomasi*	*Longistrongylus* spp.		*Longistrongylus sabie*	*Longistrongylus schrenki*	*Longistrongylus meyeri*	*Cooperia*-like	*Cooperia* spp.		*Cooperia hungi*	*Cooperia yoshidai*
				A	L4	♀	♂	♂	♂	L4	♀	♂	♂	♂	♂	♂	L4	♀	♂	♂	♂	L4	♀	♂	♂	♂
Steenbok	*Malelane* October '82	Adult	♂	0	104	1 854	—	0	1 412	0	820	0	0	260	210	—	0	42	11	—	0	—	—	—	—	—
	Riekerts Laager November '79	Young adult	♂	121	0	0	—	0	0	78	342	0	50	250	0	—	5	22	0	—	2	—	—	—	—	—
	Kalahari October '84	Adult	♂	0	0	0	—	0	0	0	50	10	0	0	0	—	0	0	0	—	0	—	—	—	—	—
Oribi	*Pretoriuskop* July '79	Adult	♂	0	0	0	—	0	—	22	107	—	—	30	37	0	0	0	—	—	—	13	53	—	—	34
Waterbuck	*Pretoriuskop* February '83	Adult	♀	11	25	508	305	0	—	0	0	—	—	—	—	—	0	0	—	0	—	0	1 950	—	125	375
Tsessebe	*Pretoriuskop* February '83	Old	♀	0	0	123	0	260	—	0	10	—	—	—	1	4	0	3	—	2	—	0	304	—	0	53
Gemsbok	*Kalahari* October '84	Adult	♂	0	66	352	403	25	—	0	228	128	—	—	—	—	0	25	—	—	25	0	6	1	—	—
Blue wildebeest	*Kalahari* October '84	Adult	♂	0	0	80	30	0	—	0	0	—	0	0	—	0	—	—	—	—	—	0	0	—	—	—
Springbok	*Kalahari* October '84	Young adult	♀	0	31	31	—	0	—	0	32	—	—	31	—	—	0	0	—	—	—	35	—	—	—	—
	October '84	Young adult	♂	0	271	50	—	2	—	0	179	—	—	103	—	—	0	0	—	—	—	0	—	—	—	—
Red hartebeest	*Kalahari* October '84	Old	♂	—	0	426	250	0	—	0	25	25	—	—	—	—	—	—	—	—	—	0	1	1	—	—

—	Not known to occur in this host
A	Adult
L4	4th stage larvae
+	Slight infestation
++	Moderate infestation

TABLE 3 The helminth burdens of grazing antelope and of grazing and browsing antelope from various localities *(continued)*

Species	Locality and date	Age	Sex	*Cooperia fuelleborni*	*Cooperioides antidorci*		*Paracooperia serrata*		*Impalaia* spp.		*Impalaia nudicollis*	*Impalaia tuberculata*	*Parabronema* spp.		*Oesophagostomum columbianum*			*Skrjabinema* spp.	*Strongyloides* spp.	*Setaria* spp.	*Agriostomum equidentatum*			*Avitellina*	*Moniezia expansa*	*Stilesia hepatica*	Total helminth burden
				♂	♀	♂	♀	♂	L4	♀	♂	♂	♀	♂	L4	♀	♂	A	♀	♀	L4	♀	♂				
Steenbok	*Malelane* October '82	Adult	♂	—	—	—	0	0	0	688	0	357	—	—	0	0	0	20	—	0	—	—	—	0	0	++	5 778
	Riekerts Laager November '79	Young adult	♂	—	—	—	0	0	10	71	0	50	—	—	0	0	0	70	—	2	—	—	—	3	2	0	1 078
	Kalahari October '84	Adult	♂	—	—	—	60	80	0	0	0	0	—	—	0	0	0	9 080	—	0	—	—	—	0	0	0	9 280
Oribi	*Pretoriuskop* July '79	Adult	♂	15	—	—	—	—	0	97	0	61	—	—	0	1	4	—	—	3	—	—	—	0	—	0	477
Waterbuck	*Pretoriuskop* February '83	Adult	♀	525	—	—	—	—	0	150	0	75	—	—	8	0	25	—	—	0	—	—	—	—	0	+	4 082
Tsessebe	*Pretoriuskop* February '83	Old	♀	0	—	—	—	—	0	29	0	52	1	1	—	—	—	125	—	0	—	—	—	—	—	—	968
Gemsbok	*Kalahari* October '84	Adult	♂	—	—	—	905	943	457	832	530	—	—	—	0	0	0	—	650	0	1	250	50	0	0	—	5877
Blue wildebeest	*Kalahari* October '84	Adult	♂	—	—	—	—	—	—	—	—	—	—	—	0	0	0	—	0	—	0	0	0	0	0	0	110
Springbok	*Kalahari* October '84	Young adult	♀	—	93	49	131	96	0	30	41	0	—	—	0	0	0	—	0	—	0	30	0	—	0	—	630
	October '84	Young adult	♂	—	62	57	439	340	0	32	71	0	—	—	0	0	0	—	236	—	0	10	10	—	0	—	1 862
Red hartebeest	*Kalahari* October '84	Old	♂	—	—	—	—	—	0	527	251	—	87	182	0	0	0	—	0	—	—	—	—	—	0	0	1 774

—	Not known to occur in this host
A	Adult
L4	4th stage larvae
+	Slight infestation
++	Moderate infestation

and composition. The only parasites found in all 3 animals were *I. tuberculata* and *C. yoshidai*. The latter was described from a reedbuck *Redunca arundinum* by Mönnig (1939), but has subsequently also been recovered from mountain reedbuck *Redunca fulvorufula* (Baker & Boomker, 1973), and blesbok (Evans, 1978; Horak, Brown, Boomker, De Vos & Van Zyl, 1982b), while the former is one of the commonest nematodes of antelope (Boomker, 1977; Gibbons, Durette-Desset & Daynes, 1977). Despite the fact that the antelope had similar feeding habits and shared the same habitat, only the host-specificity shown by the parasites can be offered to explain the differences in the helminth composition and burdens.

Longistrongylus thalae (syn. *Pseudomarshallagia thalae*) has been found in an oribi (Gibbons, 1981) and Bindernagel & Todd (1972) have recorded *Trichostrongylus* spp. from the same host.

Of the helminths listed as occurring in oribi (Round, 1968) only 3 are mentioned by Ortlepp (1961). They are *H. contortus* and *Onchocerca* sp., for which no localities were recorded, and *Setaria scalprum*, which was recorded from South Africa (Ortlepp, 1961). No comparisons can therefore be made and all the worms recovered in this study should be considered new parasite records for this antelope.

H. bedfordi has been recovered from sheep artificially infested with larvae obtained from the faeces of a waterbuck in the Johannesburg Zoological Gardens (Le Roux, 1930b). Its presence in naturally infested waterbuck is herewith confirmed.

No previous listing of the parasites of the tsessebe could be found in the literature and the results obtained in this study cannot be compared with those of other surveys.

Blue wildebeest

Horak, De Vos & Brown (1983) published the results of a survey of the parasite of blue wildebeest from the KNP. A small number of *H. bedfordi* only were recovered from the blue wildebeest from the KGNP. The same species were found in the animals from the KNP but because of insufficient data no comparisons could be made.

Springbok

Horak, Melzer & De Vos (1982a) listed the parasites they found in springbok from the western Transvaal and the western Cape Province and De Villiers, Liversidge & Reinecke (1985) those of springbok from a farm near Kimberley in the north-western Cape Province, respectively.

All the worms found in this survey are known parasites of springbok. Fewer species and lower burdens were, however, found in this survey than were found in the surveys conducted by Horak *et al.* (1982a) and De Villiers *et al.* (1985). This is ascribed to the extremely arid conditions in the KGNP.

Gemsbok and red hartebeest

Other than those published by Round (1968), no records of helminths of gemsbok and red hartebeest from South Africa exist in the literature. The gemsbok harboured a greater variety and a larger burden than the red hartebeest, which could be the result of different feeding habits.

General considerations

Of the above-mentioned animals, grey and blue duikers, bushbuck, nyala and kudu are almost exclusively browsers, feeding on the leaves, fruits and seeds of a large variety of woody plants and forbs (Dorst & Dandelot, 1972). Grass is seldom eaten by these antelope and then only when it is young and succulent or in the absence of browse (Hofmann, 1973). Giraffe are exclusively browsers feeding particularly on the shoots, leaves, flowers and pods of the leguminous trees, often to a height of 6 m above ground (Dorst & Dandelot, 1972). Steenbok, springbok and gemsbok are both grazers and browsers and will even dig for roots and tubers, while oribi, waterbuck, blue wildebeest, red hartebeest and tsessebe are grazers and will only occasionally feed on the leaves and shoots of dicotyledonaceous plants (Dorst & Dandelot, 1972).

When the mean helminth burdens of the antelope in this survey are compared, the following emerges: the 20 browsers harbour a mean of 887 worms, the 5 grazers 1 390,8 and the 6 mixed feeders, i.e. both grazing and browsing antelope, 4 063,5 worms. Giraffe are not included here because of their specialized feeding behaviour and because they are not antelope. We think that the feeding habits and the habitat preferences are responsible for these differences.

Grey duikers favour almost any kind of habitat with the exception of dense forests and deserts. The reason for their low helminth burdens have been commented on by Boomker *et al.* (1983).

Blue duiker are found exclusively in dense forest (Dorst & Dandelot, 1972) and, in the KNP, bushbuck and nyala favour the riverine or hillside forests and thick bush. Kudu are usually found in open savannah, but also occur in dense bush or light forest (Dorst & Dandelot, 1972). Within their chosen habitat the animals may roam considerably and are consequently subject to reinfestation with their own parasites to a limited extent only. Furthermore, apart from kudu and nyala, which occur in family groups, all the other antelope occur singly or in pairs, and are hence unlikely to contaminate their environment to any significant degree. It is usually only when animals are sick or injured that they stay in one place and become infested with their own parasites, with a resulting increase in helminth burdens. This was presumably the case with bushbuck No. 3, whose burden was considerably higher than the mean for the 3 bushbuck from Pafuri.

Bushbuck No. 9 had 4 102 worms, 3 215 of which were *D. harrisi*. This is the highest total worm burden for bushbuck from Skukuza. The bushbuck frequently visited the gardens of the residents of the staff village at Skukuza. Since these are watered regularly, favourable conditions for the survival of the infective larvae are probably created. Conversely, bushbuck No. 5, a very old male taken at the same locality, harboured no worms. This is possibly due to increased immunity after prolonged exposure. Michel (1963) found that resistance to the establishment of infestation developed in calves after prolonged exposure to *Ostertagia ostertagi*. It is possibly also true for *O. harrisi*, provided that the parasite elicits the same immune response as that evoked by *O. ostertagi*. Although the resistance to *O. ostertagi* differs markedly from that of *H. contortus* (=*H. placei*), a similar comparison could probably be made in the case of *H. vegliai* in bushbuck and *H. contortus* (=*H. placei*) in cattle (Fitzsimmons, 1969).

On the other hand, immunity is hardly likely to eliminate the entire worm burden and it is also quite possible that the burdens of browsing antelope are never large enough to elicit an immune response. In the latter case, bushbuck No. 5 may simply have lost whatever infestation it had and did not become reinfested.

Although giraffe are often found in herds (Dorst & Dandelot, 1972) their feeding habits are such that they will not easily become infested with the nematodes regularly occurring in antelope. They could, however, acquire these helminths when grazing, though such acquisition occurs very seldom, if at all; for instance, during droughts when they are forced to graze to survive.

Steenbok, being both grazers and browsers, could conceivably become infested with the parasites of both groups of artiodactylids. However, the present limited data do not indicate this. Because steenbok often dig for roots and tubers, they could easily become infested with the anoplocephalid tapeworms that use oribatid mites as intermediate hosts. This appears to be the case in the steenbok from Riekerts Laager, but not in the animal from the KNP. In addition, *Stilesia hepatica* was found in the grey duikers from the KNP, and the tapeworm fragments found in the liver of the waterbuck are probably those of *S. hepatica*. This indicates that the grazers and the antelope that browse at ground level are the ones most likely to become infested with the anoplocephalid tapeworms.

An interesting finding is the occurrence of an unidentified *Parabronema* sp. in the waterbuck from the KNP and in the gemsbok and the red hartebeest from the KGNP. *Parabronema* spp. are known to occur in rhino and giraffe. The waterbuck was shot in the rhino camp, where a number of white rhino, *Ceratotherium simmum* are kept, but not giraffe. Neither giraffe nor rhino are present in the KGNP, and no explanation can be offered for the presence of the *Parabronema* sp. in these antelope.

From this study it appears that many of the helminths of antelope are not very host specific. This is borne out by the fact that *T. instabilis* occurred in bushbuck, the steenbok, the tsessebe and the oribi from the KNP. *T. falculatus* was recovered from bushbuck, the steenbok from the KNP and Riekerts Laager, and the oribi. *I. tuberculata* occurred in the steenbok from the KNP and Riekerts Laager, the oribi, the waterbuck and the tsessebe, while *I. nudicollis* occurred in the gemsbok, both the sprinbok and the red hartebeest from the KGNP. *C. yoshidai* occurred in the oribi, the waterbuck and the tsessebe, and *C. hungi* was found in the oribi and the waterbuck. A *Parabronema* sp. was found in the waterbuck, the gemsbok and the red hartebeest. The helminths from the giraffe, however, were not found in any of the antelope, nor were the worms of the antelope found in the giraffe.

It seems as if the antelope tolerate each other's helminths, an indication of a well-developed host-parasite relationship resulting from long-standing associations.

The fencing of game reserves and game parks limit the natural movements of animals and confine them to a limited space where they may easily become infested with each other's worms. It also appears from this and other studies (Horak, 1980; Boomker *et al.*, 1983) that antelope are better hosts for the parasites of domestic animals than domestic animals are for those of antelope.

ACKNOWLEDGEMENTS

We wish to express our gratitude to the Board of Curators, National Parks Board and Messrs M. Opperman and W. H. du Plessis for placing the animals at our disposal. Our thanks are also due to mesdames E. L. Visser and S. A. Kingsley and Messrs C. Cheney, B. D. de Klerk and N. H. Jonker for their technical assistance and assistance with the autopsies.

This project was funded by the University of Pretoria and the Council for Scientific and Industrial Research.

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Printed by the Government Printer, Private Bag X85, Pretoria, 0001

Onderstepoort J. vet. Res., 56, 51–57 (1989)

PARASITES OF SOUTH AFRICAN WILDLIFE. III. HELMINTHS OF COMMON REEDBUCK, *REDUNCA ARUNDINUM*, IN NATAL

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ABSTRACT

BOOMKER, J., HORAK, I. G., FLAMAND, J. R. B. & KEEP, M. E., 1989. Parasites of South African wildlife. III. Helminths of common reedbuck, *Redunca arundinum*, in Natal. *Onderstepoort Journal of Veterinary Research*, 56, 51–57 (1989)

Twenty-six common reedbuck, *Redunca arundinum*, were shot in pairs at monthly intervals for 13 consecutive months in the Himeville region of Natal. Ten nematode species, 2 cestodes and 1 trematode were recovered from these animals. *Cooperia yoshidai* was both the most numerous and most prevalent worm and peak burdens occurred during summer.

Thirty-one reedbuck, killed at different intervals in various localities within the St. Lucia Reserve, harboured between 4 and 11 nematode species, 1 cestode and 1 trematode. With the exception of 4 reedbuck shot during January 1987, in which *Haemonchus contortus* was the most abundant worm, *C. yoshidai* was again both the most abundant and most prevalent worm. Peak burdens of this nematode occurred during autumn to spring.

The helminths of 5 impala, *Aepyceros melampus*, also shot in the St. Lucia Reserve were examined. Some of the worm species of impala were also found in the reedbuck from the same locality and the helminths of the 2 antelope species are compared.

An amended list, which includes several new records of the parasites of common reedbuck in South Africa is provided.

INTRODUCTION

The ecology and habits of common reedbuck, *Redunca arundinum*, have briefly been discussed by Horak, Keep, Flamand & Boomker (1988).

The helminth parasites of reedbuck in Africa have been listed by Round (1968). The helminths of these antelope in the Republic of South Africa are given by Mönnig (1924, 1928, 1931, 1939), Ortlepp (1961), Round (1968), Keep (1983) and Boomker, Keep, Flamand & Horak (1984). The present paper provides an amended list of the helminth parasites of reedbuck in the Republic of South Africa.

Howard (1983) required freshly killed reedbuck for his detailed study of the species in Natal, and the opportunity was taken during the later stages of his project to collect the helminth parasites of 26 of the animals from the Himeville region. Permission was also obtained from the Natal Parks, Fish and Game Preservation Board to shoot 31 reedbuck and 5 impala, *Aepyceros melampus*, at different localities in the St Lucia Reserve. The helminths recovered from the reedbuck from the 2 localities and trends in their seasonal abundance are discussed in this paper, while the ectoparasites of the same animals have been recorded by Horak *et al.* (1988).

MATERIALS AND METHODS

The study areas

Both the study areas fall within the summer rainfall region, as illustrated by Reinecke (1983), and have been described by Horak *et al.* (1988).

The animals

Himeville

Two reedbuck, 1 adult and 1 sub-adult were shot each month for 13 consecutive months from May 1983 to May 1984. Their sexes depended on availability and 4 adult males, 9 adult females, 10 sub-adult males and 3 sub-adult females were collected.

The St. Lucia Reserve

One adult male, 1 adult female and 2 juvenile reedbuck of either sex were shot in the Eastern Shores Nature Reserve (ESNR) at 3-monthly intervals from March 1983 to April 1984. A further 2 reedbuck, 1 adult male and 1 adult female and 2 impala were shot in the St. Lucia Game Park during May 1984. Two male reedbuck were shot during August 1984 in an area in the ESNR where buffalo occur and 4 more reedbuck, an adult male, an adult female and 2 juveniles as well as 3 impala were shot at Charters Creek, which lies within the St. Lucia Reserve, during August 1984. Four more reedbuck were shot in the ESNR during January 1987 after a number of animals had been culled because of overpopulation.

Collection of parasites

The lungs, hearts and livers of all the antelope from Himeville were processed for worm recovery as described by Horak (1978) and the abomasa, the small intestines and the large intestines as described by Reinecke (1973).

As a water-bath was not available, the bottles containing the hearts, lungs, livers and digests of the reedbuck from the St. Lucia Reserve were placed in the sun, or, on cold or overcast days, near an open fire until the desired temperature of 40–43 °C was reached. They were then moved into the shade or away from the fire until the temperature dropped by 3–5 °C, whereafter they were shaken and returned to the sun or the fire. After sieving, the residues of the hearts, lungs and livers, as well as the digests were examined *in toto* under a stereoscopic microscope. One aliquot, representing 1/10th of the volume of the ingesta, was made separately for each of the abomasa, small intestines and large intestines and also examined under a stereoscopic microscope.

The adult worms were cleared in lactophenol and identified under a standard microscope with Nomarski's differential interference contrast illumination. The descriptions of the authors listed in Table 1 were used for the identification of the worms. This table also lists the worms recovered to date from common reedbuck in South Africa. In cases where more than 1 species of a genus was encountered, the males, but not the females, were identified specifically. Fourth stage larvae and trematodes were mostly identified only to generic level.

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Received 15 November 1988—Editor

TABLE 1 Amended list of the helminth parasites of common reedbuck in the Republic of South Africa with reference to the first record and the authors used to assist with the identification

Helminth species	First record	Identification
Trematodes		
Paramphistomum spp. Fischoeder, 1901	This paper	Eudardo, 1982
Cestodes		
Cysticercus sp. (*sic*)	Ortlepp, 1961	*
Moniezia benedeni Blanchard, 1891	This paper	Skrjabin & Spasski, 1963
Taenia hydatigena larvae	This paper	Verster, 1969
Nematodes		
Bunostomum cobi Maplestone, 1931	Ortlepp, 1961	*
Bunostomum trigonocephalum Railliet, 1902	Mönnig, 1928	*
Bunostomum sp.	Boomker *et al.*, 1984	†
Cooperia fuelleborni Hung, 1926	Ortlepp, 1961	*
Cooperia neitzi Mönnig, 1932	Ortlepp, 1961	*
Cooperia yoshidai Mönnig, 1939	Mönnig, 1939	Gibbons, 1981
Gaigeria sp. females	This paper	Ortlepp, 1937
Dictyocaulus viviparus Railliet & Henri, 1907	Boomker *et al.*, 1984	Yorke & Maplestone, 1926
Haemonchus contortus Cobb, 1898	Ortlepp, 1961	Gibbons, 1979
Haemonchus vegliai Le Roux, 1929	Ortlepp, 1961	*
Longistrongylus sabie Travassos, 1937	Ortlepp, 1961	*
Longistrongylus schrenki Ortlepp, 1939	Boomker *et al.*, 1984	Gibbons, 1977
Oesophagostomum columbianum Curtice, 1890	Mönnig, 1931	*
Ostertagia ostertagi Ransom, 1907	This paper	Ransom, 1911
Setaria bicoronata Railliet & Henri, 1911	This paper	Yeh, 1959
Setaria boulengeri Thwaite, 1927	Thwaite, 1927	*
Setaria hornbyi Boulenger, 1921	Mönnig, 1924	*
Setaria labiatopapillosa Railliet & Henri, 1911	Veglia, 1919	Yeh, 1959
Trichostrongylus colubriformis Ransom, 1911	Boomker *et al.*, 1984	†
Trichostrongylus falculatus Ransom, 1911	This paper	Ransom, 1911
Trichuris sp. females	This paper	Yorke & Maplestone, 1926

* = After Round (1968). Not found in this survey

† = Not found in this survey

TABLE 2 The helminths recovered from 26 common reedbuck from Himeville

Helminth species	Number of worms recovered			Number of animals infested
	Larvae	Adults	Total	
Paramphistomes	*	1 494	1 494	17
Moniezia benedeni	*	1	1	1
Taenia hydatigena	3	*	3	3
Cooperia yoshidai	317	37 969	38 286	22
Dictyocaulus viviparus	0	203	203	14
Gaigeria sp.	0	50	50	2
Haemonchus contortus	575	1 080	1 655	11
Longistrongylus schrenki	0	2 065	2 065	17
Ostertagia ostertagi	0	101	101	3
Setaria bicoronata	0	54	54	6
Setaria labiatopapillosa	0	1	1	1
Trichostrongylus falculatus	3	75	78	3
Trichuris sp. females	0	25	25	1
Mean nematode burden	34	1 601	1 635	—

* = Not found in reedbuck
— = Not applicable

RESULTS

Himeville

The helminths recovered from reedbuck from this region are listed in Table 2 and their seasonal abundance is graphically illustrated in Fig. 1.

Ten nematode species, 2 cestodes and 1 trematode were recovered. Of these, *Cooperia yoshidai* was both the most abundant and most prevalent nematode. One specimen of *Moniezia benedeni* was found in 1 of the animals and 3 others each harboured 1 larva of *Taenia hydatigena*. Paramphistomes were recovered from 17 animals.

The largest burden of 9 676 worms was recovered from an adult female shot during July 1983 and the smallest burden of 50 worms from a sub-adult male shot during May 1984. Only 1 animal, a sub-adult female shot during August 1983 did not harbour any worms.

The St. Lucia Reserve

The helminths recovered from the reedbuck shot in this reserve are listed in Table 3 and their seasonal abundance is illustrated in Fig. 2.

Nine nematode species, 1 cestode and 1 trematode were recovered from the 19 animals shot from March 1983 to April 1984 in the ESNR. The most abundant worm was *C. yoshidai* and the most prevalent worms were *Haemonchus contortus* and *Longistrongylus schrenki*.

The 4 reedbuck collected during January 1987 from the ESNR harboured only 4 nematodes species, of which

TABLE 3 The helminths recovered from common reedbuck from the St. Lucia Reserve

Helminth species	Number of worms recovered			Number of animals infested
	Larvae	Adults	Total	
Eastern Shores (19 animals)				
Paramphistomes	*	183	183	1
Moniezia benedeni	*	1	1	1
Cooperia yoshidai	4 422	59 114	63 536	16
Dictyocaulus viviparus	0	818	818	17
Gongylonema sp.	0	8	8	2
Haemonchus contortus	12 070	11 716	23 786	18
Longistrongylus schrenki	3 414	5 956	9 370	18
Oesophagostomum columbianum	1	51	52	3
Setaria bicoronata	0	194	194	14
Skrjabinema sp.	0	14 524	14 524	7
Trichuris sp. females	0	25	25	1
Mean nematode burden	1 048	4 863	5 911	
Eastern Shores, buffalo area (2 animals)				
Cooperia yoshidai	401	6 436	6 837	2
Dictyocaulus viviparus	0	311	311	2
Gongylonema sp.	0	7	7	1
Haemonchus contortus	1 803	700	2 503	2
Longistrongylus schrenki	502	1 055	1 557	2
Oesophagostomum sp. females	—	25	25	1
Setaria sp. females	—	6	6	1
Skrjabinema sp.	0	976	976	1
Mean nematode burden	1 353	4 758	6 111	
St. Lucia Game Park (2 animals)				
Cooperia hungi	†	101	101	1
Cooperia yoshidai	†	7 075	7 075	2
Cooperioides hepaticae	†	5	5	1
Cooperia-like	101	9 209	9 310	2
Dictyocaulus viviparus	0	293	293	2
Gongylonema sp.	0	1	1	1
Impalaia tuberculata	0	251	251	2
Longistrongylus schrenki	37	1 536	1 573	2
Oesophagostomum sp.	28	0	28	2
Setaria bicoronata	0	41	41	2
Skrjabinema sp.	0	11 156	11 156	2
Mean nematode burden	83	14 834	14 917	
Charters Creek (4 animals)				
Cooperia yoshidai	17 625	43 164	60 789	4
Dictyocaulus viviparus	0	278	278	4
Haemonchus contortus	1 167	2 330	3 497	4
Longistrongylus schrenki	0	333	333	3
Setaria sp. females	0	61	61	4
Skrjabinema spp.	0	10 650	10 650	1
Mean nematode burden	4 698	14 204	18 902	
Eastern Shores, January 1987 (4 animals)				
Cooperia yoshidai	10	64	74	2
Gaigeria sp. females	0	10	10	1
Haemonchus contortus	40	594	634	4
Longistrongylus schrenki	731	99	830	3
Mean nematode burden	195	192	387	

* = Not found in reedbuck
— = Not applicable
† = Larvae and females counted together as *Cooperia*-like

L. schrenki was the most abundant and *H. contortus* the most prevalent.

Eight nematode species were recovered from the 2 reedbuck from the buffalo area of the ESNR. *C. yoshidai* was the most abundant and together with *H. contortus*, *L. schrenki* and *Dictyocaulus viviparus*, occurred in both antelope.

Eleven nematode species, of which *Cooperia* spp. were the most abundant, were recovered from the reedbuck in the St. Lucia Game Park.

Only 6 nematode species were recovered from the antelope from Charters Creek. *C. yoshidai* was the most numerous and together with *D. viviparus*, *H. contortus* and a *Setaria* sp. occurred in all 4 animals.

The helminths recovered from the impala from the 2 localities are listed in Table 4.

Fifteen species of nematodes and 1 trematode were recovered from the impala from the St. Lucia Game Park. The *Cooperia* spp. together with the 2 *Coo-*

TABLE 4 The helminths recovered from impala from the St. Lucia Reserve

Helminth species	Number of worms recovered			Number of animals infested
	Larvae	Adults	Total	
St. Lucia Game Park (2 animals)				
Paramphistomes	*	1	1	1
Agriostomum sp. females	—	25	25	1
Cooperia fuelleborni	†	84	84	2
Cooperia hungi	†	204	204	2
Cooperia yoshidai	†	1 106	1 106	2
Cooperia spp. females	—	1 884	1 884	2
Cooperioides hamiltoni	†	236	236	2
Cooperioides hepaticae	†	85	85	2
Cooperia-like larvae	135	—	135	2
Dictyocaulus viviparus	0	18	18	1
Gaigeria pachyscelis	0	77	77	1
Haemonchus contortus	193	2 246	2 439	2
Impalaia tuberculata	82	1 795	1 877	2
Longistrongylus schrenki	0	290	290	2
Oesophagostomum sp.	104	50	154	2
Ostertagia sp.	0	153	153	2
Strongyloides papillosus	0	450	450	1
Trichostrongylus spp. females	—	75	75	1
Mean nematode burden	257	4 602	4 859	
Charters Creek (3 animals)				
Cooperioides hamiltoni	0	60	60	3
Haemonchus contortus	166	1 130	1 296	3
Longistrongylus schrenki	397	316	713	1
Trichostrongylus angistris	†	1	1	1
Trichostrongylus thomasi	†	119	119	3
Trichostrongylus instabilis	†	10	10	1
Trichostrongylus spp.	0	247	247	3
Mean nematode burden	187	628	815	

† = Larvae indistinguishable at species level and counted together
— = Not applicable
* = Not found in impala

perioides spp. were the most numerous, followed by *H. contortus,* and *Impalaia tuberculata*. Both antelope were infested with these nematodes.

Seven nematodes were recovered from the impala from Charters Creek. Of these, *H. contortus* was the most numerous, followed by *L. schrenki* and *Trichostrongylus* spp.

DISCUSSION

Himeville

D. viviparus is normally a definitive parasite of cattle and according to Reinecke (1983), it occurs particularly on irrigated pastures in isolated areas in the mist belt of the Drakensberg of Natal and the Transvaal, as well as in the western Cape Province. It has also been recovered from several antelope species, including reedbuck (Horak, De Vos & Brown, 1983; Boomker *et al.*, 1984). *D. viviparus* infestation seems to be common in the Himeville area. This is borne out by the fact that the 2 reedbuck previously examined for parasites (Boomker *et al.*, 1984) as well as 14 out of 26 antelope examined during this survey harboured this worm. A reedbuck from Midmar Dam and 1 from Estcourt, however, did not harbour these parasites (Boomker *et al.*, 1984). The free-living stages of this nematode are sensitive to heat and desiccation but are resistant to cold. Himeville falls within the mist belt of the Natal Drakensberg, where the winters are severe but the summers moderate. These environmental conditions appear to be favourable for the survival of the infective stages of this lungworm (Oakley, 1979; Reinecke, 1983; Boomker *et al.*, 1984).

H. contortus is a parasite of sheep, goats and cattle, but like *D. viviparus* has been recorded from many antelope species (Horak, 1981; Horak, Brown, Boomker, De Vos & Van Zyl, 1982; Horak, De Vos & De Klerk, 1982; Boomker, Du Plessis & Boomker, 1983; Horak *et al.*, 1983; Boomker *et al.*, 1984; Boomker, Horak & De Vos, 1986). According to the criteria set by Horak (1980, 1981), these helminths, together with *C. yoshidai,* and *Setaria bicoronata* could be considered definitive parasites of reedbuck. The occasional parasites seem to be the *Trichuris* spp., and the accidental parasites *O. ostertagi, Setaria labiatopapillosa* and *Trichostrongylus falculatus*.

Of a grand total of 44 166 helminths recovered from the 26 reedbuck, 38 286 were adult *C. yoshidai* and 4th stage *Cooperia* sp. larvae. Large numbers of *C. yoshidai* are to be expected in reedbuck since it is the type host (Mönnig, 1939), and trends in the seasonal abundance of the nematodes of reedbuck in the present survey seem to be due to *C. yoshidai* only.

The largest burden of 9 000 *C. yoshidai* was present in 1 of the animals shot during July 1983 (Fig. 1). The infective larvae of the *Cooperia* spp. are resistant to desiccation and to low temperatures (Reinecke, 1983) and can overwinter on irrigated pastures. Since reedbuck are known to utilize irrigated pastures in this area during winter (Howard, 1983), it is conceivable that the large burden in this animal was acquired from the pastures.

Smaller peaks of *C. yoshidai* were observed in reedbuck during October, November and December 1983 (Fig. 1) and we are of the opinion that these peaks reflect the true situation. This agrees with Hobbs (1961), who recorded peak egg counts due to *Cooperia* spp. in calves in Natal during spring and summer, and with Boomker, Keep & Horak (1987), who recovered peak numbers of a *Cooperia* sp. in bushbuck and grey duiker in the same province during these seasons.

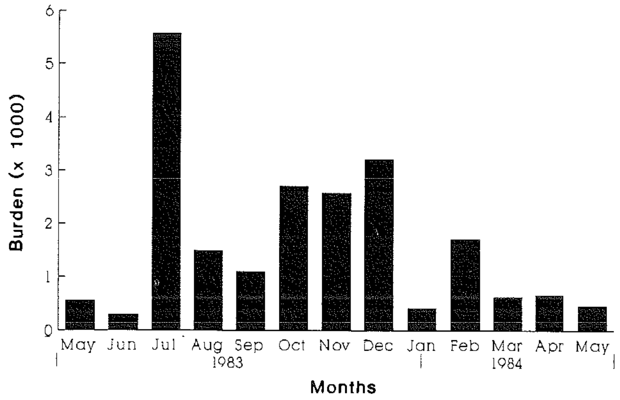

FIG. 1 The seasonal abundance of nematodes in common reedbuck in the Himeville region, Natal

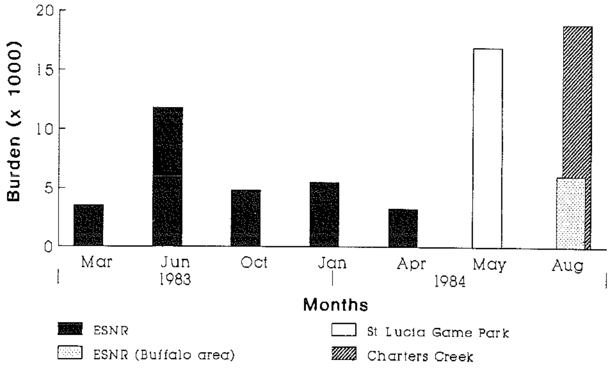

FIG. 2 The seasonal abundance of nematodes of common reedbuck in the St. Lucia Nature Reserve

Three reedbuck harboured only small numbers of *Ostertagia ostertagi*. This appears to be an accidental parasite of these animals and was probably acquired from cattle on the irrigated pastures.

Ortlepp (1939) described *L. schrenki* from a waterbuck, *Kobus ellipsiprymnus,* while Boomker *et al.* (1984) found small numbers of this parasite in reedbuck from Himeville and other regions of Natal. From the present data it appears to be fairly common in the province and should be considered a definitive parasite of reedbuck.

The mean total burden of 1 681 nematodes in the reedbuck is approximately the same as that found by Boomker *et al.* (1984) in reedbuck from other localities on the Natal midlands and should be considered the 'normal' mean burden in areas with a moderate climate.

The St. Lucia Reserve

Reedbuck

The definitive parasites of reedbuck from this locality are the same as those of reedbuck from Himeville. The occasional parasites are *Gongylonema* sp., *Skrjabinema* sp., *Trichuris* sp. and the *Oesophagostomum* spp., while the *Gaigeria* sp. and in the St. Lucia Game Park, *Cooperia hungi, Cooperioides hepaticae* and *Impalaia tuberculata* appear to be the accidental parasites.

Out of a grand total of 112 497 worms collected from the 19 animals from the ESNR, 63 533 (56,5 %) were *C. yoshidai* and their 4th stage larvae. In the ESNR (buffalo area) a total of 12 220 worms was recovered, of which 6 838 were *C. yoshidai* and their larvae. No trematodes or cestodes were recovered from the animals from the other localities within the St. Lucia Reserve. The reedbuck at Charters Creek harboured a total of 75 610 worms, of which 60 791 were *C. yoshidai* and their larvae. *C. yoshidai* constituted less than 50 % of the burdens of the reedbuck from the St. Lucia Game Park. Out of a total of 33 890 nematodes, 16 485 were *C. yoshidai* and 11 156 *Skrjabinema* sp.

The seasonal abundance of the helminths recovered from the reedbuck from the various localities within the St. Lucia Game Reserve are illustrated in Fig. 2.

The largest numbers of *C. yoshidai* in the antelope from the ESNR occurred in June 1983 and was due to one animal harbouring more than 10 000 worms. Large burdens of *C. yoshidai* also occurred in the reedbuck from the St. Lucia Game Park shot during May 1984 and in those from Charters Creek, shot in August 1984. From the present limited data it appears that *C. yoshidai* occurs in peak numbers during the cooler months of the year in reedbuck in the ESNR (May–August).

Despite the sensitivity of the free-living stages of *D. viviparus* to desiccation and heat, this nematode was present in the majority of the antelope in the St. Lucia Reserve, where the winters are mild and the summers hot, albeit in slightly smaller numbers than in the Himeville region with its severe winters and mild summers. This is in accordance with Reinecke's (1983) observation that the parasites are rife on irrigated pastures, to which the ESNR with its seasonally inundated grasslands and high rainfall could be likened.

There are 3 known species of *Skrjabinema* that parasitize the ruminants of this country. They are *Skrjabinema ovis, Skrjabinema africana* and *Skrjabinema alata* (Mönnig, 1932). As *S. africana* was described from 3 immature females and *S. alata* from 7 females only, we were unable to identify the *Skrjabinema* species found in this survey. These nematodes appear to be apathogenic, despite large numbers being present (11 081 in a reedbuck from the St. Lucia Game Park).

Trichuris sp., *Oesophagostomum columbianum,* and *I. tuberculata* are ubiquitous nematodes that have been recovered from a large variety of antelope (Round, 1968; Boomker, 1977; Gibbons, Durette-Desset & Daynes, 1977; Horak *et al.*, 1983).

C. hungi and *C. hepaticae* are nematodes that are primarily parasites of impala. Their presence in reedbuck in the St. Lucia Game Park is probably due to cross-infestation.

Impala

The 3 impala from Charters Creek harboured considerably fewer worms than the reedbuck. Presumably, this is because impala are mixed feeders, browsing frequently in between grazing periods, while reedbuck will only browse during winter or droughts, when grass is not readily available. We assume that reedbuck ingest more infective larvae on the grazing than do impala.

One of the impala from Charters Creek harboured a single male *Trichostrongylus angistris,* a nematode only recently described from the red duiker, *Cephalophus natalensis,* from this reserve (Boomker & Vermaak, 1986). The nematode has so far been recovered only from red duiker and its presence in impala is therefore a new record.

General considerations

The definitive parasites of reedbuck in Natal appear to be *C. yoshidai, D. viviparus, H. contortus, L. schrenki* and *Setaria* spp., all of which were recovered from antelope from the various localities. In the majority of cases, *C. yoshidai* was both the most abundant and the most prevalent, with *D. viviparus*, *H. contortus* or *L. schrenki* occupying second, third or fourth place.

An interesting pattern as regards the total worm burdens from the different localities emerged from this study. The antelope from Himeville had the smallest mean burden, namely, 1 635 worms. We assume that the reedbuck population density in this region is such that the pasture does not become contaminated to any significant degree and that the regular treatment of the domestic stock with anthelmintics indirectly serves to limit the burdens in the antelope. Furthermore, the severe winters in the region cause many of the free-living stages to die.

The reedbuck from the ESNR and the area in the ESNR where buffalo occur had mean burdens of 5 911 and 6 111 worms respectively. The burdens are approximately 3,6–3,7 times that of the reedbuck from Himeville, indicating that the environmental conditions are more suitable for the survival of the free-living stages. It is also possible that because the population density of the reedbuck (0,46 per ha) is higher here than at Himeville, the environment is contaminated to a greater degree, ultimately leading to higher burdens.

The 4 reedbuck shot during January 1987 in the ESNR had a significantly lower total helminth burden, 387 as opposed to the approximately 6 011 worms in the antelope shot earlier. This may have been due to fewer infective larvae on the veld because of a smaller antelope population after some culling had taken place.

The antelope from the St. Lucia Game Park had a larger variety of worms and the mean burden was 14 917. This is approximately 9 times that of the reedbuck from Himeville and 2,5 times that of the antelope from the ESNR. The presence of worms such as *C. hungi, C. fuelleborni, C. hepaticae* and *I. tuberculata,* which are parasites of a number of other antelope species, including impala but excluding reedbuck, indicates that cross-infestation took place to a much greater degree than in the other localities. The Game Park is fenced and the population density of 0,86 reedbuck per ha is such that they, and presumably the other antelope species as well, are infested with each other's worms to a significant degree. It appears that host-specificity is largely absent in this park.

The lack of diversity in helminth species and the large mean burden in the reedbuck from Charters Creek is possibly the result of the few other grazing antelope that occur there as well as the high population density of 0,86 animals per ha. The reedbuck appear to be infested with their own host-specific worms and considering the mean burden of 18 902 worms, which is approximately 11,5 times that of the antelope from Himeville, considerable numbers of infective larvae must continually be present. Although the burden consists mainly of *C. yoshidai,* of which the pathogenicity is unknown, we are of the opinion that too many reedbuck are present and that some animals may have to be removed.

ACKNOWLEDGEMENTS

We thank the Director, Natal Parks, Game and Fish Preservation Board and the Director of Forestry, Directorate of Environmental Affairs, for placing the animals at our disposal. We also thank Dr P. C. Howard during whose project the antelope at Himeville were shot and who assisted with the collection of the parasites. Thanks are also due to the staff of the Natal Parks, Game and Fish Preservation Board, particularly those at Mission Rock and Charters Creek, for their assistance. Mr Dick Nash, Warden of the St. Lucia Reserve is thanked for supplying us with information about the reserve.

This project was partly funded by the Council for Scientific and Industrial Research.

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Parasites of South African wildlife. XIV. Helminths of nyalas (*Tragelaphus angasii*) in the Mkuzi Game Reserve, KwaZulu-Natal

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ABSTRACT

BOOMKER, J., BOOYSE, D.G., WATERMEYER, R., DE VILLIERS, I.L., HORAK, I.G. & FLAMAND, J.R.B. 1996. Parasites of South African wildlife. XIV. Helminths of nyalas (*Tragelaphus angasii*) in the Mkuzi Game Reserve, KwaZulu-Natal. *Onderstepoort Journal of Veterinary Research*, 63:265–271

The helminths of 58 nyalas (*Tragelaphus angasii*) culled in the Mkuzi Game Reserve, KwaZulu-Natal, during March 1991, and six culled during March 1994, were collected, identified and counted. Of these, an as yet undescribed *Camelostrongylus* sp., *Cooperia hungi*, an *Onchocerca* sp., *Strongyloides papillosus* and *Moniezia benedeni* are new parasite records.

The individual nematode burdens of the antelope examined during March 1991 varied from one to 2 327, and the total mean adult gastro-intestinal-nematode burden was 586. Those examined during March 1994 had burdens that varied from 322 to 1 778, with a mean of 854. The two *Camelostrongylus* spp. were the most prevalent nematodes in the nyalas culled during 1991, while the trematode *Cotylophoron jacksoni* was most prevalent in those culled during 1994. The most numerous nematode in nyala calves during 1991 was a *Cooperia rotundispiculum* race, while the two *Camelostrongylus* spp. were most numerous in the adult and sub-adult nyalas from both surveys.

No clear trends between rainfall and nematode burdens were evident, nor was there any correlation between faecal nematode egg counts and nematode burdens. Contrary to what was observed in an earlier survey, female nyalas had larger nematode burdens than the males.

Keywords: Helminths, nyala, parasites, *Tragelaphus angasii*, wildlife

INTRODUCTION

The internal parasites of nyalas (*Tragelaphus angasii*) were listed by Dixon (1964), Round (1968), Vincent, Hitchins, Bigalke & Bass (1968), Keep (1971), Boomker (1986), Boomker, Horak & De Vos (1986) and Boomker, Horak & Flamand (1991). The last-named authors reported on the helminths of 77 nyalas in four nature reserves in KwaZulu-Natal, including Mkuzi Game Reserve.

As part of the ongoing surveys of the helminth parasites of wild animals in South Africa, culling programmes of nyalas in the Mkuzi Game Reserve, northern KwaZulu-Natal, were attended during March

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Accepted for publication 30 July 1996—Editor

1991 and March 1994, and the helminth parasites of 58 and of six nyalas, respectively, collected. In this paper, the results of these collections are presented and compared with those of the previous survey conducted in this reserve. An amended host-parasite list is also provided.

MATERIALS AND METHODS

The geophysiology of the Mkuzi Game Reserve has been described by Boomker *et al.* (1991). In summary, the Reserve (27°33′–27°46′S; 32°07′–32°19′E, altitude 130–300 m), is approximately 25 091 ha in extent and situated in north-eastern KwaZulu-Natal. The vegetation of the higher altitudes is classified as Lowveld, while that of the lower altitudes consists of Coastal Forest and Thornveld (Acocks 1988). Rain falls mostly during summer, and summers are hot and often humid, while winters are mild. Frost seldom occurs.

A total of 58 nyalas, comprising 24 adults, 12 sub-adults and 22 calves, were shot during March 1991. The gastro-intestinal tracts (excluding the fore-stomachs) of 26 of these antelope were processed for helminth recovery, as described by Boomker, Horak & De Vos (1989) and the mucosae digested. Helminths were collected only from the abomasa and the proximal one-third of the small intestines of the remaining 32 antelope, and the respective mucosae digested. Neither the hearts, lungs nor livers of these antelope were examined for the presence of helminths.

Separate aliquots, each representing one-tenth of the volume of the ingesta of the abomasa, small intestines and large intestines, were made and examined under a stereoscopic microscope. The mucosal digests were examined *in toto*. All the worms were removed, identified and counted.

Faecal specimens were collected from the rectums of the antelope and duplicate faecal nematode egg counts were done, according to Reinecke's (1961) modification of the McMaster technique of Gordon & Whitlock (1939).

Three adult male and three adult female nyalas were processed for helminth recovery during March 1994, as described by Boomker *et al.* (1989). However, separate aliquots, representing only one-twentieth of the respective ingesta, were examined. The hearts and livers were not examined and the mucosae of the large intestines were not digested. Faecal specimens for nematode egg counts were not collected.

A number of the distomes recovered from the nyalas were dehydrated in graded ethyl alcohol and embedded in paraffin wax. Ventral and sagittal serial sections, 5 µm thick, were cut of the entire trematode, stained with Masson's trichrome stain (Bancroft & Stevens 1982) and mounted in Canada balsam.

Fragments of the cestode recovered from one of the nyalas examined during March 1991, were stained with aceto-alum-carmine stain. Gravid proglottides were compressed between two glass slides for better observation of the shape of the eggs.

All the helminths were identified under a standard microscope in accordance with the descriptions provided by the authors listed in Table 1.

RESULTS

The rainfall during the two months preceding and the month of parasite collection for the March 1983 as well as the 1991 and 1994 surveys, is presented in Fig. 1.

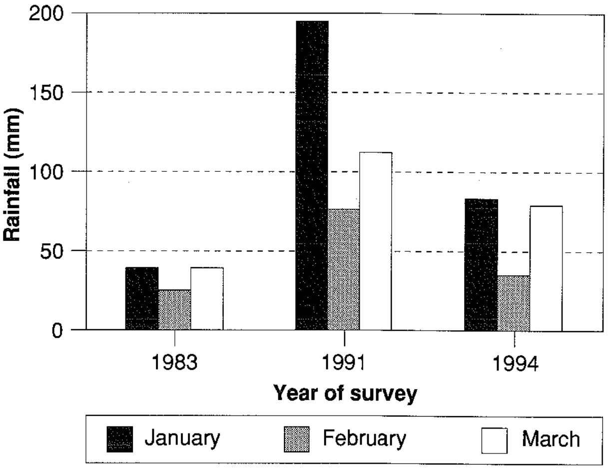

FIG. 1 Rainfall during the two months preceding and the month during which parasites were collected for each of the 1983, 1991 and 1994 surveys of the helminths of nyalas in Mkuzi Game Reserve

The *Camelostrongylus* spp. were the most numerous and accounted for 88,7% of the total adult nematode burden of the adult nyalas examined during March 1991. They were also the most prevalent, occurring in 23 out of the 24 antelope. *Paracooperia horaki* was next most numerous and prevalent (Table 2).

The sub-adult nyalas examined during March 1991 harboured three nematode genera, and seven identified to the species level. The *Camelostrongylus* spp. were the most numerous, accounting for 70 % of the adult nematode burden. They were also the most prevalent, occurring in all 12 antelope (Table 3).

Nyala calves examined during March 1991, harboured the largest variety of helminths. The two *Cooperia* spp. were the most numerous, and accounted for 47,7% of the total adult nematode burden, followed by the two *Camelostrongylus* spp. (31,4%) and *P. horaki* (10%). However, the *Camelostrongylus* spp. were the most prevalent, occurring in 20 out of the 22 antelope.

TABLE 1 Amended list of the helminth parasites of nyalas, *Tragelaphus angasii*, with reference to the first record and the authors of the descriptions used to assist with the identifications

Helminth species	First record	Identification
Trematodes		
Calicophoron calicophorum (Fischoeder, 1901) Näsmark, 1937	Ortlepp pers. comm [a]	-
Cotylophoron cotylophorum (Fischoeder, 1901) Stiles & Goldberger, 1910	Ortlepp pers. comm [a]	-
Cotylophoron jacksoni Näsmark, 1937	Dixon 1964	Eduardo 1985
Paramphistomum microbothrium (Fischoeder, 1901)	Dixon 1964	-
Schistosoma mattheei Veglia & Le Roux, 1929	Boomker *et al.* 1991	-
Cestodes		
Moniezia benedeni (Moniez, 1879) Blanchard, 1891	This paper	Taylor 1928
Taenia sp. larvae	Boomker *et al.* 1991	-
Thysaniezia sp.	Boomker *et al.* 1991	-
Nematodes		
Camelostrongylus harrisi (Le Roux, 1930) Durette-Desset, 1989	Vincent *et al.* 1968	Le Roux 1930
Camelostrongylus sp.	This paper	Boomker, unpublished data
Cooperia hungi Mönnig, 1931	This paper	Gibbons 1981
Cooperia rotundispiculum Khalil & Gibbons, 1980	Boomker 1991	Boomker 1991
Dictyocaulus viviparus (Bloch, 1782) Railliet & Henry, 1907	Keep 1971	-
Elaeophora sagittus (Von Linstow, 1907) Anderson & Bain, 1976	Ortlepp 1961	-
Gaigeria pachyscelis Railliet & Henry, 1910	Boomker *et al.* 1991	Levine 1980
Gongylonema verrucosum (Giles, 1982) Neumann, 1984	Vincent *et al.* 1968	-
Gongylonema sp.	Boomker *et al.* 1991	-
Haemonchus vegliai Le Roux,1929	Boomker *et al.* 1991	Gibbons 1979
Haemonchus sp.	Keep 1971	-
Impalaia tuberculata Mönnig, 1924	Boomker *et al.* 1991	Boomker 1977
Oesophagostomum sp.	Boomker *et al.* 1991	-
Onchocerca sp.	This paper	Anderson & Bain 1976
Paracooperia horaki Boomker, 1986	Boomker 1986	Boomker 1986
Setaria africana (Yeh, 1959) Ortlepp, 1961	Yeh 1959	Yeh 1959
Setaria labiatopapillosa (Perroncito, 1882) Railliet & Henry, 1911	Mönnig 1931	Yeh 1959
Setaria sp.	Boomker *et al.* 1991	Yeh 1959
Strongyloides papillosus (Wedl, 1856)	This paper	Ransom 1911
Teladorsagia trifurcata (Ransom, 1907)	Keep 1971	-
Trichostrongylus deflexus Boomker & Reinecke, 1989	Boomker *et al.* 1991	Boomker & Reinecke 1989
Trichostrongylus falculatus Ransom, 1911	Boomker *et al.* 1991	Ransom 1911

[a] As communicated to Round (1968)

- Not found in this survey

One trematode species, one nematode genus and three nematode species were recovered from the adult nyalas culled during March 1994. *Cotylophoron jacksoni* occurred in all six of the antelope, while the two *Camelostrongylus* spp. were the most numerous nematodes, comprising 91 % of the total adult nematode burden. Together with *P. horaki*, the *Camelostrongylus* spp. were the most prevalent nematodes, each occurring in five antelope (Table 3).

The results of the faecal nematode egg counts are presented in Table 4.

The numbers of helminths collected during March 1983, and the 1991 and 1994 surveys are compared in Table 5. From this table it is clear that the 1991 survey yielded the largest variety of helminths.

DISCUSSION

Five new helminths can be added to the existing list of parasites of nyalas. These are the *Camelostrongylus* sp., *Cooperia hungi*, an *Onchocerca* sp., *Strongyloides papillosus* and *Moniezia benedeni*.

Camelostrongylus harrisi is a common parasite of nyalas and has been found in all the previous surveys (Boomker *et al.* 1986, 1991). The recent discovery of a new species is in line with the concept of major and minor species as observed between *Teladorsagia circumcincta* and *Teladorsagia trifurcata* of sheep (Lancaster & Hong 1981). *Camelostrongylus harrisi* would appear to be the major species in nyalas, because its numbers were 20–30 % higher than

TABLE 2 Helminths recovered from 58 nyalas culled during March 1991

Helminth species	Number of helminths recovered			Number of animals infected
	Larvae	Adults	Total	
Adults (24 animals)				
Camelostrongylus harrisi	0	4 733	4 733	23
Camelostrongylus sp.	0	2 997	2 997	22
Cooperia hungi	0	20	20	1
Cooperia rotundispiculum	0	211	211	2
Cooperia females	0	73	73	3
Cooperia type larvae	390	–	390	2
Gaigeria pachyscelis	0	1	1	1
Ostertagia type larvae	84	–	84	5
Onchocerca sp.	–	1	1	1
Paracooperia horaki	0	679	679	16
Mean nematode burden	20	363	383	
Subadults (12 animals)				
Camelostrongylus harrisi	0	3 201	3 201	12
Camelostrongylus sp.	0	2 072	2 072	12
Cooperia hungi	0	869	869	2
Cooperia rotundispiculum	0	637	637	4
Cooperia type larvae	22	–	22	1
Haemonchus vegliai	0	36	36	3
Ostertagia type larvae	284	–	284	6
Paracooperia horaki	0	713	713	8
Setaria africana	0	3	3	3
Trichostrongylus deflexus	0	3	3	1
Mean nematode burden	25	628	653	
Calves (22 animals)				
Cotylophoron sp. immature	1	0	1	1
Moniezia benedeni	0	1	1	1
Camelostrongylus harrisi	0	3 749	3 749	20
Camelostrongylus sp.	0	1 821	1 821	20
Cooperia hungi	0	2 280	2 280	14
Cooperia rotundispiculum	0	6 169	6 169	14
Cooperia type larvae	1 395	–	1 395	7
Gaigeria pachyscelis	0	23	23	2
Haemonchus vegliai	0	460	460	9
Impalaia tuberculata	420	1 173	1 593	6
Ostertagia type larvae	50	–	50	4
Paracooperia horaki	0	1 774	1 774	19
Setaria sp.	0	1	1	1
Strongyloides papillosus	0	163	163	5
Trichostrongylus deflexus	0	11	11	1
Trichostrongylus falculatus	0	96	96	5
Trichostrongylus females	0	10	10	1
Mean nematode burden	85	806	891	

– Not applicable

those of the new species in all the surveys conducted. Together with a *Cooperia rotundispiculum* race and *P. horaki*, the two *Camelostrongylus* spp. were the definitive parasites of nyalas in the 1983 survey (Boomker *et al.* 1991). The 1991 and 1994 surveys confirm this observation.

Cooperia hungi is a common parasite of impalas, *Aepyceros melampus* (Horak 1978) and should be regarded as an accidental parasite of nyalas. The worms were found only in the 1991 survey, and then mostly in calves. The presence of *Strongyloides papillosus* only in calves, and then only in low numbers, suggests that this infestation may be milk-borne, as proposed for impalas (Horak 1978) and kudus (Boomker *et al.* 1989). Both the *Onchocerca* sp. and *Moniezia benedeni* can be regarded as accidental parasites.

TABLE 3 Helminths recovered from six adult nyalas culled during March 1994

Helminth sp.	No. of helminths recovered			No. of nyalas infected
	Larvae	Adults	Total	
Cotylophoron jacksoni	0	1 901	1 901	6
Camelostrongylus harrisi	0	3 019	3 019	5
Camelostrongylus sp.	0	1 649	1 649	5
Camelostrongylus females	–	20	20	1
Cooperia rotundispiculum	0	120	120	1
Paracooperia horaki	0	317	317	5
Mean nematode burden	0	854	854	

– Not applicable

TABLE 4 Total adult female nematode and total nematode burdens, and faecal nematode egg count of nyalas culled during March 1991

Female nyalas				
Animal number and age	Total adult female nematode burden	Total nematode burden	Faecal nematode egg count (eggs/g)	
			Count 1	Count 2
Adults				
5	74	144	0	0
6	152	250	0	0
13	471	891	0	0
15	178	279	0	0
27	395	730	0	0
32	18	61	200	300
33	340	648	300	100
36	54	96	0	0
39	249	359	0	0
42	679	1 047	0	0
48	329	586	0	0
50	399	552	200	100
55	524	891	0	0
Mean	297	503	54	38
Subadults				
31	50	136	0	0
38	691	1 143	200	100
44	704	1 129	0	0
45	270	782	0	0
54	350	774	0	100
Mean	413	793	40	40
Calves				
1	821	1 506	200	0
2	30	61	0	0
14	501	957	800	600
18	1 355	2 327	100	200
24	593	860	0	0
25	475	807	0	0
40	337	751	0	0
49	351	710	200	200
52	756	1 342	200	300
57	881	1 662	400	200
58	145	239	200	300
Mean	568	1 020	191	164

Male nyalas				
Animal number and age	Total adult female nematode burden	Total nematode burden	Faecal nematode egg count (eggs/g)	
			Count 1	Count 2
Adults				
4	33	57	0	0
7	46	48	0	200
19	66	82	0	0
20	85	195	0	0
23	155	223	0	0
26	134	198	0	0
28	0	1	0	0
30	294	686	0	0
41	71	179	0	0
43	49	61	0	0
47	226	343	0	0
Mean	105	188	0	18
Subadults				
10	242	444	0	0
17	33	44	0	0
29	572	1 083	200	200
37	239	392	0	0
51	191	337	0	0
53	523	898	300	200
56	299	369	0	0
Mean	300	510	71	57
Calves				
3	151	218	0	0
8	276	584	0	0
9	461	944	0	0
11	212	317	0	0
12	421	598	0	0
16	206	364	0	0
21	911	1 743	0	0
22	176	366	300	400
34	95	210	0	0
35	268	584	0	0
46	282	579	0	0
Mean	314	592	27	36

TABLE 5 Comparison of the results of the helminth surveys of nyalas conducted during March 1983, 1991 and 1994

Helminth species	Results of surveys conducted		
	1983 (n = 4)	1991 (n = 58)	1994 (n = 6)
Paramphistomes	3 432	1	1 901
Moniezia benedeni	–	1	–
Cooperia rotundispiculum	2 040	7 017	120
Cooperia hungi	–	3 169	–
Cooperia spp. females	–	73	–
Cooperia type larvae	0	1 807	–
Elaeophora sagittus	0	–	–
Gaigeria pachyscelis	1	24	–
Haemonchus vegliai	75	496	–
Haemonchus larvae	0	–	–
Impalaia tuberculata	0	1 173	–
Impalaia larvae	0	420	–
Camelostrongylus harrisi	15 331 [a]	11 683	3 019
Camelostrongylus sp.	112	6 890	1 649
Camelostrongylus females	–	–	20
Ostertagia type larvae	100	418	–
Onchocerca sp.	–	1	–
Paracooperia horaki	802	3 166	317
Setaria sp.	4	1	–
Setaria africana	–	3	–
Strongyloides papillosus	–	163	–
Trichostrongylus deflexus	–	14	–
Trichostrongylus falculatus	44	96	–
Trichostrongylus spp. females	–	10	–
Mean adult gastro-intestinal nematode burden	4 601	586	854

– Not found during that particular survey

[a] One animal harboured 13 293 *Camelostrongylus* spp. adults

Although good rain fell during January 1991, it did not appear to affect the mean adult nematode burden of the adult nyalas. It might, however, have affected the burdens in the younger animals, because in the subadults and calves they were 1,7 and 2,3 times, respectively, that of the adult nyalas. In the 1983 survey, male nyalas had larger burdens than the females (Boomker *et al.* 1991). However, in both the 1991 and 1994 surveys, the females had the larger burdens, but since only small numbers of helminths were involved, the differences are probably not significant.

It is clear that little correlation exists between the total female or total helminth burdens, and faecal nematode egg counts of nyalas. Similar results have been obtained for kudus in the Kruger National Park (Boomker *et al.* 1989), thereby indicating that faecal egg counts should not be used to determine the nematode population status of antelope in game reserves.

On comparing the results of the 1983, 1991 and 1994 surveys, it is apparent that the nyalas culled during 1983 had the largest mean burden, but this is owing to one of the antelope harbouring a large number of *Camelostrongylus harrisi*. If this animal is left out of the calculations, the mean adult nematode burden becomes 1 227, which is not much larger than the 854 of the 1994 survey. The nyalas culled during 1991 had the largest variety of helminths and the smallest burdens, while the six antelope culled during 1994 had the smallest variety of helminths and a mean burden intermediate to that of the other groups. This may have been brought about by climatic conditions or a slight overpopulation of nyalas during 1983. However, the magnitudes of the total burdens are insignificant, and when the species diversity is taken into account, they should in no way be detrimental to the antelope.

ACKNOWLEDGEMENTS

We wish to thank the Director of the Natal Parks Board for placing the animals at our disposal, and the staff of Mkuzi Game Reserve for their assistance.

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Parasites of South African wildlife. XV. Helminths of scrub hares, *Lepus saxatilis* in the Kruger National Park

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ABSTRACT

BOOMKER, J., HORAK, I.G. & BOOYSE, D.G. 1997. Parasites of South African wildlife. XV. Helminths of scrub hares, *Lepus saxatilis,* in the Kruger National Park. *Onderstepoort Journal of Veterinary Research*, 64:285—290

A total of 145 scrub hares from three localities in the Kruger National Park were examined for helminths: 124 at Skukuza, 15 at Shingwedzi, and three each at Pretoriuskop and Pafuri. *Trichostrongylus deflexus* was the most prevalent and most abundant nematode, and was collected from hares from all four localities. *Trichostrongylus falculatus* was present in three localities. *Trichostrongylus thomasi* and *Dermatoxys vlakhaasi* occurred only at Skukuza in 50 and 23 %, respectively, of the hares examined. The cestode *Mosgovoyia pectinata* and the nematode genus *Impalaia* were each recovered from three localities and *Cooperia hungi* from two. There was no apparent seasonal pattern of abundance of the worms, and the intensities of infection of male and female hares were similar. With the exception of *D. vlakhaasi,* all the helminths recovered in this study represent new records for scrub hares in South Africa.

Keywords: Helminths, *Lepus saxatilis*, parasites, scrub hares, wildlife

INTRODUCTION

Scrub hares, *Lepus saxatilis*, are widely distributed throughout Africa except in forested areas. In southern Africa they are absent from the western coastal desert and the eastern coastal forests as well as from the arid country bordering the Orange River (Skinner & Smithers 1990). They prefer savannah woodland or scrub where there is grass cover, but they do not occur on open grassland. They are common in agriculturally developed areas, especially those where crops are grown, and in derelict lands where there is bush regeneration. Scrub hares are mostly nocturnal and apparently sensitive to the weather, as they are not in evidence on cold nights. They are grazers, living on the leaves, stems and rhizomes of preferably green grass (Skinner & Smithers 1990).

The helminth parasites of hares have received little attention in this country. Ortlepp (1937, 1938b) described *Dermatoxys vlakhaasi* and *Inermicapsifer leporis*, from Cape hares, *Lepus capensis*, and Neitz (1965) lists *Coenurus serialis* collected from an unspecified hare by Ortlepp (1938a). This paper records the helminths collected from scrub hares at four localities in the Kruger National Park.

MATERIALS AND METHODS

Survey localities and animals

The hares examined in this survey are the same as those from which ectoparasites were collected at Shingwedzi, Pafuri and Pretoriuskop, and during the first two years of the ectoparasite survey at Skukuza (Horak, Spickett, Braack & Penzhorn 1993; Louw, Horak & Braack 1993). These authors also provide details on the vegetation types of the localities. The

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Accepted for publication 30 October 1997—Editor

particulars of the hares available to us and the localities at which they were collected are provided in Table 1.

All hares were processed for helminth recovery as described by Boomker, Horak & De Vos (1989), but digests of the mucosae of the stomach and intestines were not done. Female *Trichostrongylus* spp. were proportionally assigned to the males that occurred in each host. However, some hares harboured only female *Trichostrongylus* spp. and these have not been assigned to a species.

The ecological terms used here are in accordance with those of Margolis, Esch, Holmes, Kuris & Schad (1982) and the term 'average' is defined as the total number of parasites from all the hosts divided by the number of hosts in which the parasites are present.

RESULTS

Skukuza

The climatological data for Skukuza are graphically represented in Fig. 1. The average monthly intensities of the helminth infections are listed in Table 2 and the monthly fluctuations in the total *Trichostrongylus* spp. burdens are graphically illustrated in Fig. 2.

Six nematode species and one cestode species were collected from these hares. Of the nematodes *Trichostrongylus deflexus* (prevalence 96,8 %, range 40–9 563) was the commonest, followed by *Trichostrongylus thomasi* (prevalence 50,4 %, range 23–1 796), *Trichostrongylus falculatus* (prevalence 48,0 %, range 28–2 693), *Impalaia tuberculata* (prevalence 32,0 %, range 10–520) and *Dermatoxys vlakhaasi* (prevalence 23,3 %, range 1–120). Two hares each harboured 20 *Cooperia hungi*. One hare harboured 60 female *Trichostrongylus* spp. that could not be assigned to a species, one a single *Trichostrongylus* sp. larva, and another 20 *D. vlakhaasi* larvae. Three hares, one a juvenile female, the others two adult males, had no worms, while the range varied from 40–9 900 worms in the 121 (97,6 %) animals that were infected. The cestode *Mosgovoyia pectinata* was present in 22 hares (prevalence 17,7 %, range 1–17).

None of the helminths showed discernible seasonal trends, neither according to rainfall nor to minimum or maximum temperatures, and the intensities of infection between male and female hares, although very variable, were similar.

The prevalences of trichostrongylid nematodes in hares at Skukuza are compared in Table 3 with those in kudus, *Tragelaphus strepsiceros*, examined south and west of Skukuza from April 1981 to March 1983 (Boomker *et al.* 1989), and in impalas, *Aepyceros melampus* (Boomker, Horak & De Vos, unpublished data 980), and warthogs, *Phacochoerus africanus* (Horak, Boomker, De Vos & Potgieter 1988). The impalas and warthogs were examined from January 1980 to January 1981 and both species were shot in the same locality as the hares.

The scrub hares and impalas harboured five helminth species, and hares, kudus and warthogs harboured four species in common.

Pretoriuskop

Only *I. tuberculata* (prevalence 100 %, range 4–400), *T. deflexus* (prevalence 66 %, range 89–244), *T. falculatus* (prevalence 66 %, range 95–671) and *M. pectinata* (prevalence 66 %, range 1–14) were present in hares from this locality.

Shingwedzi

The average bimonthly burdens of the 15 hares from this locality are listed in Table 1. Four species of nematodes were collected, of which *I. tuberculata* (range 20–80) and *T. deflexus* (range 20–144) were both present in nine hares, *T. falculatus* in five, unidentified *Trichostrongylus* spp. females in two, and *C. hungi* in one. Fourteen hares harboured nematodes and a single animal two *M. pectinata*. No seasonal pattern of abundance was evident for either the individual nematode species or the entire worm burdens.

Pafuri

One of the three hares harboured 340 *T. deflexus* only, while no worms were present in the remaining two animals.

DISCUSSION

With the exception of *D. vlakhaasi*, all the helminths recovered in this study represent new parasite records for scrub hares in South Africa. *D. vlakhaasi* was originally described from a Cape hare by Ortlepp (1937) as *Heteroxinema vlakhaasi*. However, Quentin (1975) transferred this species to the genus *Dermatoxys*, a parasite exclusive to the Leporidae. Its presence in scrub hares is therefore to be expected and it should be regarded as a definitive parasite.

C. hungi is primarily a parasites of antelopes, in which it occurs commonly but in varying numbers, impala being the preferred hosts (Table 2). It was encountered in only one out of 41 warthogs examined in the Northern Province (Boomker, Horak, Booyse & Meyer 1991) and in none in the Kruger National Park (Horak *et al.* 1988). In view of its low prevalence and low intensity in the monogastric herbivores, including hares, it should be considered an accidental parasite in these animals.

I. tuberculata was originally described from an impala (Mönnig 1924). Subsequently it has been collected from a variety of antelopes (Boomker 1977, 1991) as well as from warthogs (Horak *et al.* 1988; Boomker *et al.* 1991). It was also recovered in very low numbers from all six red rock rabbits, *Pronolagus* sp., examined in Kenya by Fukumoto, Kamiya & Suzuki (1980) and should be considered a definitive parasite of hares and possibly rabbits. Its wide host spectrum indicates its tolerance of a variety of physiological environments.

Trichostrongylus spp. utilize a large variety of terrestrial vertebrates, notably birds and herbivorous mammals, as hosts. They seem to have evolved separately in domesticated and in wild animals, where different species occupy the same niches (Anderson 1992). For instance, *Trichostrongylus axei* is found in the abomasa of sheep, goats and cattle and the stomachs of domestic pigs and horses (Reinecke 1983), and *T. thomasi* in the abomasa of several wild ruminants (Boomker 1991) and the stomachs of warthogs (Horak *et al.* 1988; Boomker *et al.* 1991), zebras (Krecek, Malan, Reinecke & De Vos 1987) and now hares.

The presence of *Trichostrongylus* spp. in hares and rabbits is well known. Fukumoto *et al.* (1980) recorded *Trichostrongylus colubriformis* in 100 % *Pronolagus* sp. but the maximum number of worms collected from a single host was only 31, which is considerably fewer than the various *Trichostrongylus* spp. recovered from hares from all the localities in this study. Boag (1987) records the prevalence of *Trichostrongylus retortaeformis* in *L. capensis* and *Oryctolagus cuniculus* in Scotland as being 73,8 % and 80 %, respectively. The maximum number of worms he collected was 2 730 from a hare and 4 325 from a rabbit. Allgöwer (1992) found the same parasite in 92 % of *Lepus europaeus* in the upper Rhine Valley, Germany. These figures are reasonably similar to those for the hares from Skukuza.

In the Kruger National Park, scrub hares and impalas are the preferred hosts of *T. deflexus*, and warthogs

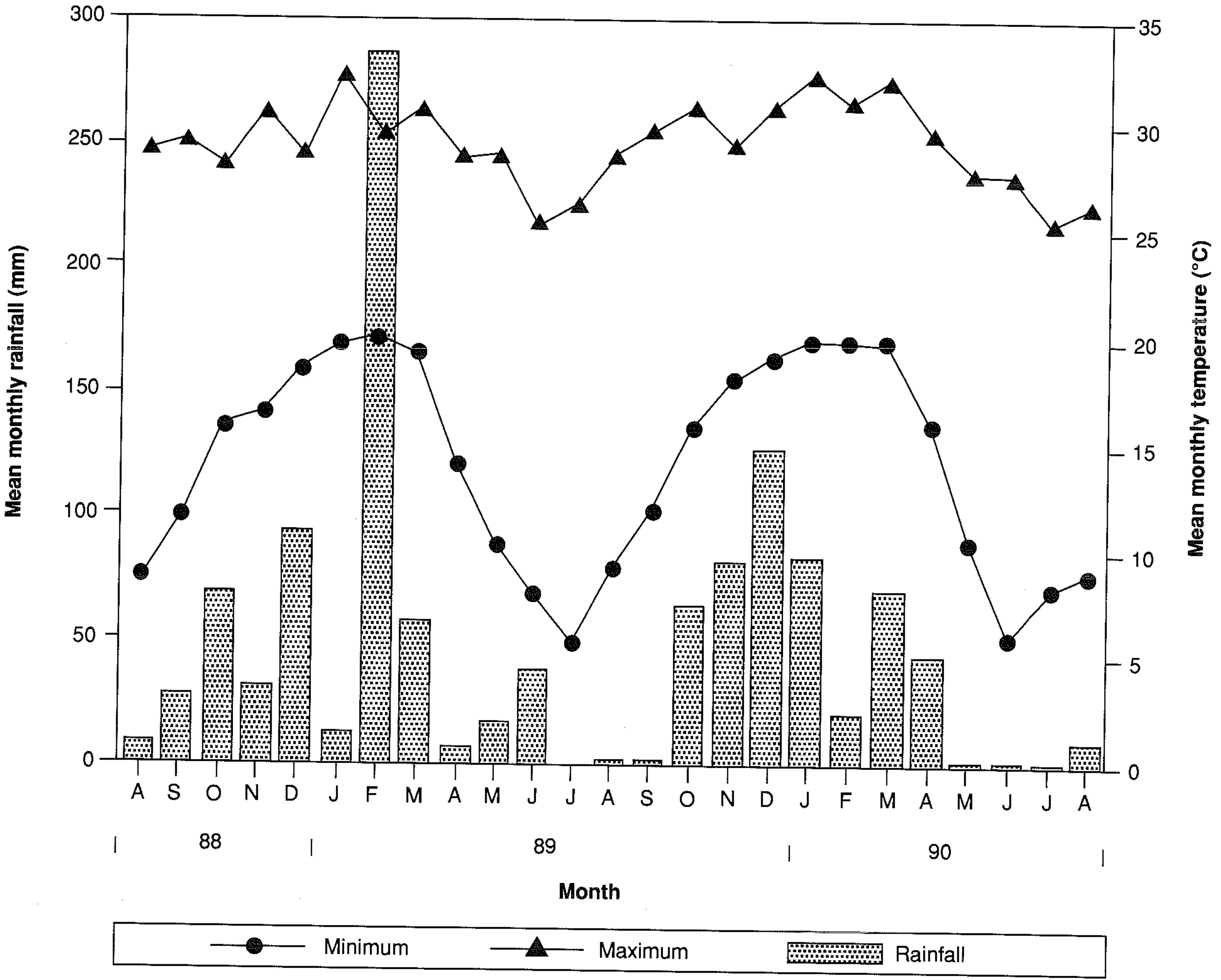

FIG. 1 Mean monthly rainfall, and mean monthly minimum and maximum temperatures measured at Skukuza for the period August 1988 to August 1990

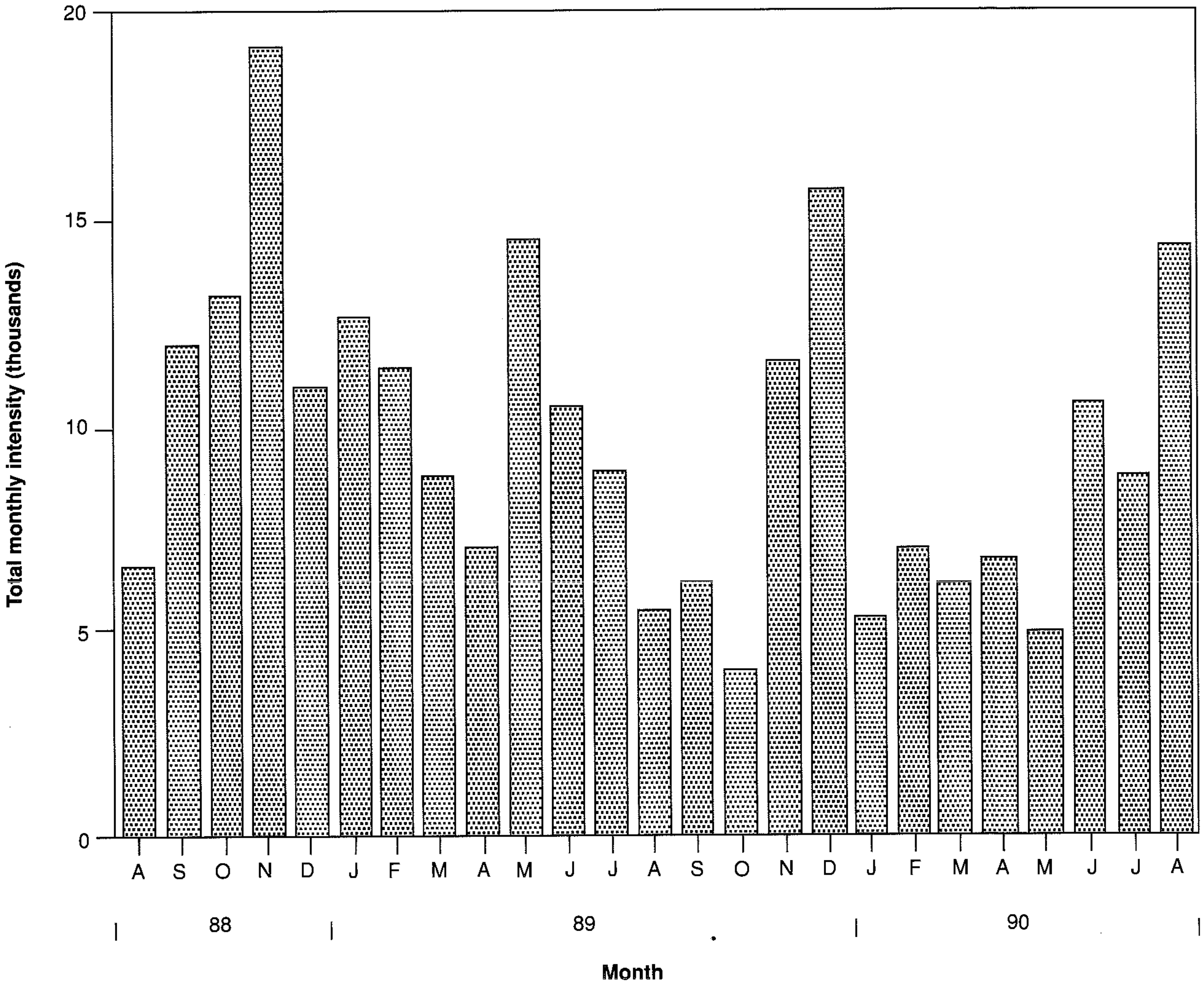

FIG. 2 Monthly fluctuations of the total *Trichostrongylus* spp. burdens of scrub hares at Skukuza during the period August 1988 to August 1990

TABLE 1 Collection data of scrub hares in the Kruger National Park

Locality	Grid reference	Section of Park	Frequency	Date collected	Ages and sex[b]				Number collected
					JF	SAF	AF	AM	
Skukuza	24°58′S,31°36′E	South	Five per month[a]	Aug 1988 – Aug 1990	2	–	35	87	124
Pretoriuskop	25°10′S,31°16′E	Sout-hwest	In one month	June 1989	–	–	2	1	3
Shingwedzi	23°07′S,31°26′E	North	Three bimonthly	Aug 1989 – Aug 1990	–	1	10	4	15
Pafuri	23°27′S,31°19′E	Far north-east	One per month	Feb 1990 – Apr 1990	–	1	2	–	3

[a] Excepting August 1988 when four were examined

[b] JF = Juvenile female; SAF = Sub-adult female; AF = Adult female; AM = Adult male

the preferred host of *T. thomasi*, while kudus appear to be poor hosts for *T. falculatus* and apparently do not harbour *T. thomasi* (Table 2). The high prevalence and incidence of *T. thomasi* in warthogs is surprising because it is considered a definitive parasite of wild ruminants. It now seems possible that the nematode is primarily a parasite of the monogastric herbivores and has secondarily adapted to ruminants.

The anoplocephalid tapeworm *M. pectinata* is a cosmopolitan parasite of the Lagomorpha and is the only one of the five species of the genus that occurs in

TABLE 2 The average monthly or bimonthly intensities of nematode infections of scrub hares, *Lepus saxatilis*, from Skukuza and Shingwedzi, Kruger National Park

Locality and month collected[a]	*Cooperia hungi*	*Impalaia tubercula*		*Trichostrongylus*				*Dermatoxys vlakhaasi*		Average monthly total nematode burden
		Adults	Larvae	*deflexus*	*falculatus*	*thomasi*	Females	Adults	Larvae	
Skukuza										
Aug. 1988: Males (3)	0	114	0	1 004	0	0	130	8	0	1 256
Females (1)	0	40	0	2 090	0	0	0	1	0	2 131
Sep. 1988: Males (5)	0	42	2	2 378	0	9	0	0	10	2 440
Oct. 1988: Males (3)	0	27	0	3 588	0	86	0	0	40	3 740
Females (2)	0	5	0	1 067	0	23	0	0	10	1 105
Nov. 1988: Males (3)	0	13	0	2 557	0	110	0	0	0	2 680
Females (2)	10	10	0	5 519	0	22	0	0	0	5 560
Dec. 1988: Males (2)	0	0	0	2 500	0	0	0	20	0	2 520
Females (3)	0	0	0	1 927	0	53	0	13	0	1 993
Jan. 1989: Males (2)	0	60	0	3 274	0	177	0	90	0	3 600
Females (3)	7	67	0	1 894	0	19	0	0	0	1 987
Feb. 1989: Males (5)	0	12	0	2 209	0	63	0	0	0	2 284
Mar. 1989: Males (4)	0	45	0	1 966	18	91	0	0	0	2 150
Females (1)	0	120	0	340	0	0	0	0	0	460
Apr. 1989: Males (3)	0	13	7	166	81	0	0	7	0	273
Females (2)	0	0	0	2 911	191	48	0	0	0	3 140
May 1989: Males (2)	0	0	0	1 682	1 402	97	0	10	0	3 191
Females (3)	0	7	0	2 432	168	106	0	0	0	2 713
Jun. 1989: Males (4)	0	0	0	2 101	318	81	0	0	0	2 500
Females (1)	0	0	0	175	245	0	0	0	0	420
Jul. 1989: Males (3)	0	0	0	1 883	348	16	0	7	0	2 253
Females (2)	0	0	0	703	206	152	0	0	0	1 061
Aug. 1989: Males (3)	0	20	0	1 265	131	17	20	0	0	1 453
Females (2)	0	10	0	529	0	72	0	0	0	610
Sep. 1989: Males (2)	0	0	0	1 805	59	306	0	10	0	2 180
Females (3)	0	20	0	563	29	8	0	7	0	627
Oct. 1989: Males (4)	0	5	0	793	163	30	0	5	0	995
Females (1)	0	0	0	0	0	0	0	0	0	0
Nov. 1989: Males (5)	0	116	0	2 010	226	64	0	4	0	2 420
Dec. 1989: Males (2)	0	0	0	2 431	626	124	0	0	0	3 180
Females (3)	0	93	0	2 426	634	33	0	0	0	3 186
Jan. 1990: Males (2)	0	0	0	486	18	37	0	0	0	540
Females (3)	0	27	0	1 232	153	15	0	0	0	1 427
Feb. 1990: Males (5)	0	0	0	965	267	186	0	0	0	1 388
Mar. 1990: Males (5)	0	52	0	1 173	0	47	0	8	0	1 280
Apr. 1990: Males (5)	0	8	0	1 126	89	122	0	0	0	1 344
May 1990: Males (3)	0	0	0	807	40	0	0	0	0	847
Females (2)	0	0	0	731	379	70	0	0	0	1 180
Jun. 1990: Males (5)	0	20	0	1 528	539	21	0	36	0	2 144
Jul. 1990: Males (3)	0	40	0	992	348	130	0	0	0	1 510
Females (2)	0	0	0	1 902	191	27	0	20	0	2 140
Aug. 1990: Males (4)	0	10	0	1 609	550	475	0	5	0	2 650
Females (1)	0	60	0	1 423	2 312	44	0	20	0	3 859
Shingwedzi										
Aug. 1989	0	80	0	110	60	0	0	0	0	250
Oct. 1989	0	33	0	63	47	0	60	0	0	203
Dec. 1989	0	40	0	102	36	0	60	0	0	238
Feb. 1990	40	40	0	70	0	0	0	0	0	150
Apr. 1990	0	40	0	20	0	0	0	0	0	60

[a] Figures in brackets indicate number of animals examined

TABLE 3 Comparison of the prevalence of the commonly shared trichostrongylid nematodes of scrub hares, warthogs, kudus and impalas

Host species	Helminth species and prevalence (%)				
	Cooperia hungi	*Impalaia tuberculata*	*Trichostrongylus*		
			deflexus	*falculatus*	*thomasi*
Scrub hares (*n* = 124)	1,6	32,3	96,8	48,4	50,8
Warthogs (*n* = 28)	–	3,6	14,3	3,6	75,0
Kudus (*n* = 96)	8,2	25,8	43,3	6,2	–
Impalas (*n* = 142)	87,3	72,5	86,6	24,6	57,0

Africa. It represents a new parasite record for scrub hares in this country.

ACKNOWLEDGEMENTS

We wish to thank the National Parks Board for placing the hares at our disposal, Dr L.E.O. Braack and Mr I. de Beer of the Parks Board, and Miss H. Heyne and Mr A.M. Spickett of the Onderstepoort Veterinary Institute, who assisted with the collection of the hares and the helminths. This study was funded by the Foundation for Research Development, the University of Pretoria, the Medical University of Southern Africa and the National Parks Board.

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Onderstepoort Journal of Veterinary Research, 67:31–41 (2000)

Parasites of South African wildlife. XVI. Helminths of some antelope species from the Eastern and Western Cape Provinces

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ABSTRACT

BOOMKER, J., HORAK, I.G., WATERMEYER, R. & BOOYSE, D.G. 2000. Parasites of South African wildlife. XVI. Helminths of some antelope species from the Eastern and Western Cape Provinces. *Onderstepoort Journal of Veterinary Research,* 67:31–41

The numbers and species of helminths recovered from one black wildebeest, *Connochaetes gnou,* three eland, *Taurotragus oryx,* 18 mountain reedbuck, *Redunca fulvorufula,* one red hartebeest, *Alcelaphus buselaphus* and two springbok, *Antidorcas marsupialis,* in the Mountain Zebra National Park, Eastern Cape Province; two black wildebeest, two grey rhebuck, *Pelea capreolus,* two mountain reedbuck and four springbok in the Karoo National Park, Western Cape Province; two bontebok, *Damaliscus pygargus dorcas,* two eland, two gemsbok, *Oryx gazella* and two springbok in the West Coast National Park, Western Cape Province; and a single springbok on a farm near Bredasdorp, Western Cape Province, are recorded. Nematodes belonging to a total of 12 genera and 20 species were identified. A single cestode was also recovered. Sixteen new host associations are recorded for the nematodes and one for the cestode *Moniezia benedeni. Nematodirus spathiger* had the widest host spectrum and with the exception of black wildebeest, was collected from all the host species examined.

Keywords: Antelope, helminths, nature reserves, wildlife

INTRODUCTION

The helminths of a variety of antelope from the eastern part of South Africa, mainly the Kruger National Park and the KwaZulu-Natal Game Reserves, have been surveyed and the results documented (Horak, De Vos & Brown 1983; Boomker 1990). However, with the exception of those in grysbok, *Raphicerus melanotis,* common duikers, *Sylvicapra grimmia,* kudu, *Tragelaphus strepsiceros,* grey rhebuck, *Pelea capreolus* and bontebok, *Damaliscus pygargus dorcas,* few surveys have been conducted on the internal parasites of antelopes occurring in the Eastern and Western Cape Provinces (Boomker, Horak & MacIvor 1989c; Boomker, Horak & Knight 1991a; Boomker & Horak 1992).

During the late 1980s and early 1990s the opportunity arose to collect the helminths of antelope in three nature reserves and a commercial farm in these Provinces and the results are presented here.

MATERIALS AND METHODS

Survey localities

Mountain Zebra National Park

This park (32°10′–32°18′S; 25°24′–25°30′E; Alt. 1 200–1 975 m) lies near the town of Cradock in the northern part of the Eastern Cape Province and is approximately 6 536 ha in extent. The vegetation consists of Karroid *Merxmuelleria* Mountain Veld, replaced by Karoo on the higher slopes and Karroid Broken Veld in the northern section (Acocks 1988). Rainfall is low with 70 % falling during February and

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Accepted for publication 17 December 1999—Editor

March (Fourie 1983) and the area can be described as semi-arid. Summers are warm to hot and winters cold with frost occurring regularly. Snow sometimes falls on the higher parts (Penzhorn 1975).

The park contains blesbok, *Damaliscus pygargus phillipsi,* black wildebeest, *Connochaetes gnou,* eland, *Taurotragus oryx,* gemsbok, *Oryx gazella,* mountain reedbuck, *Redunca fulvorufula,* red hartebeest, *Alcelaphus buselaphus,* grey rhebuck, steenbok, *Raphicerus campestris,* klipspringer, *Oreotragus oreotragus,* springbok, *Antidorcas marsupialis* and Cape mountain zebra, *Equus zebra zebra.*

A single black wildebeest, three eland, one red hartebeest and two springbok were shot during the period March 1983 to February 1984. In addition, two mountain reedbuck were shot at approximately three-monthly intervals from November 1983 to December 1985, a total of 18 antelope.

Karoo National Park

The park (32°12′–32°20′S; 22°25′–22°39′E; Alt. 600–1 932 m) is situated near the town of Beaufort West in the north-western part of the Western Cape Province and comprises an area of 17 706 ha. The vegetation consists of typical Karroid Broken Veld, Karroid *Merxmuelleria* Mountain Veld replaced by Karoo and Central Lower Karoo vegetation types (Acocks 1988). Like the Mountain Zebra National Park, the area can be described as semi-arid. Summers are hot to very hot and winters cold, with frost occurring commonly. Snow sometimes falls on the higher reaches.

Two black wildebeest, two grey rhebuck, two mountain reedbuck and four springbok were shot in this reserve during February 1991.

West Coast National Park

This park (33°6′–33°10′S; 17°57′–18°2′E; Alt. 0–50 m) is situated on the west coast of the Western Cape Province, approximately 120 km north of Cape Town, and comprises an area of 24 779 ha. The vegetation consists of Strandveld and isolated patches of Coastal Fynbos (Acocks 1988). The park falls within the winter rainfall region where summers are moderate to hot, and winters cold and wet.

Two bontebok, two eland, two gemsbok and two springbok were shot here during February 1990.

The farm near Bredasdorp

A single springbok ewe was shot on a commercial farm situated approximately 30 km south-east of Bredasdorp, in the southern part of the Western Cape Province. The vegetation is classified as Coastal Fynbos and Coastal Renosterveld (Acocks 1988). In addition to springbok, eland and cattle are also present on the farm.

Collection and counting of parasites

The helminths of all these animals were collected, identified and counted as described by Boomker, Horak & De Vos (1989b). No digests of the abomasal and intestinal mucosae were done on the springbok from the farm near Bredasdorp.

RESULTS

For comparative purposes, the helminths are listed per locality and host rather than locality only. The helminths from eland from the Mountain Zebra and West Coast National Parks are listed in Table 1, those from mountain reedbuck from the Mountain Zebra and Karoo National Parks in Table 2 and those from springbok from all the localities in Table 3. Helminths from bontebok from the West Coast National Park are listed in Table 4 and those from gemsbok from the West Coast National Park in Table 5. Table 6 summarizes the host spectrum of the various helminths.

TABLE 1 The helminths recovered from eland in the Mountain Zebra and West Coast National Parks

Locality, number of hosts examined and helminth species	Number of helminths recovered			Prevalence %
	Larvae	Adults	Total	
Mountain Zebra National Park (*n* = 3)				
Haemonchus mitchelli	0	250	250	33,3
Nematodirus spathiger	0	1 750	1 750	33,3
Cooperia rotundispiculum race	0	4 750	4 750	33,3
Mean total burden	0	2 250	2 250	
West Coast National Park (*n* = 2)				
Bronchonema magna	0	0	6	50,0
Cooperia rotundispiculum race	0	35 603	35 603	100,0
Mean total burden	0	17 805	17 805	

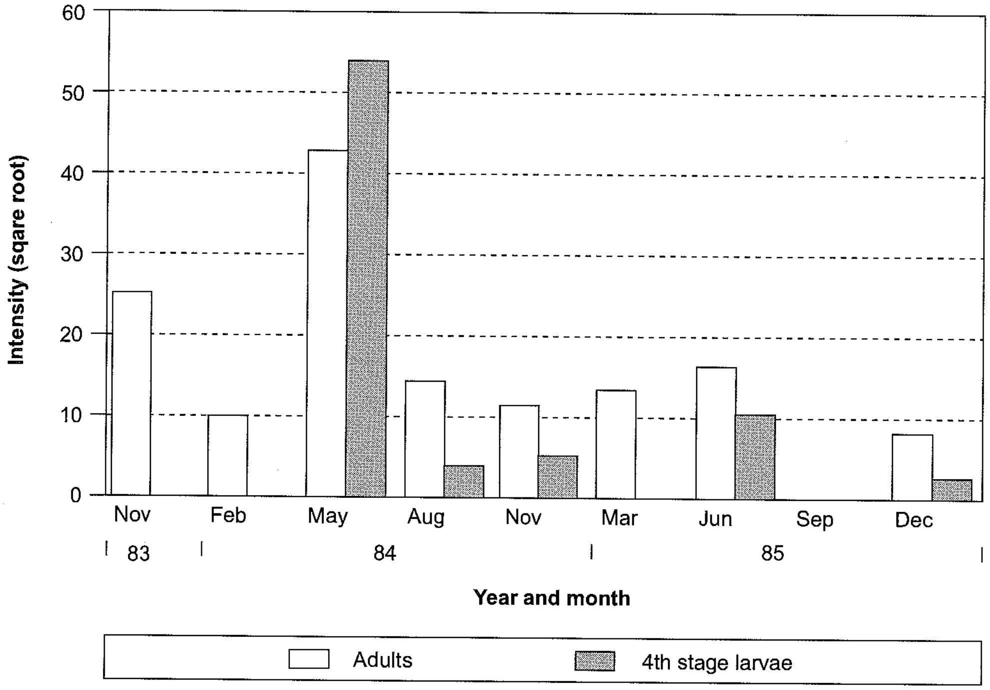

FIG. 1

Mean tri-monthly number of 4th stage and adult nematodes recovered from mountain reedbuck in the Mountain Zebra National Park. No helminths were recovered from the antelope shot during September 1985

TABLE 2 The helminths recovered from eland in the Mountain Zebra and Karoo National Parks

Locality, number of hosts examined and helminth species	Number of helminths recovered			Prevalence %
	Larvae	Adults	Total	
Mountain Zebra National Park (*n* = 18)				
Moniezia benedeni	[a]	2	2	5,5
Nematodirus spathiger	2 740	4 785	7 525	61,0
Ostertagia type females	–	1	1	5,5
Skrjabinema spp.	–	290	290	166,0
Trichostrongylus falculatus	0	20	20	5,5
Mean total nematode burden	152	283	435	
Karoo National Park (*n* = 2) No helminths were recovered	0	0	0	0

– Not applicable

[a] Do not occur in mountain reedbuck

Mountain Zebra National Park

The black wildebeest from this locality harboured a single *Taenia* sp. larva, one fourth stage *Haemonchus* sp. larva and 26 *Haemonchus* spp. females.

In eland the *Cooperia rotundispiculum* race was most numerous, accounting for 70 % of the adult nematode burden, followed by *Nematodirus spathiger* with 26 % (Table 1).

The red hartebeest harboured 1 725 *Nematodirus spathiger*, of which 325 were fourth stage larvae, as well as 100 *Trichostrongylus falculatus*. Both these nematodes are new parasite records for this host.

Four mountain reedbuck harboured no worms. The remaining 14 antelopes' burdens, including fourth stage larvae, varied from 1–7 600, the larger number occurring in a heavily pregnant female shot during May 1983. *Nematodirus spathiger* was present in 11 of the 14 mountain reedbuck that harboured worms, and was the only nematode species present in eight of the antelope. These nematodes accounted for 96 % of the number of adult nematodes present in these antelope (Table 2).

The seasonal distribution of the helminths recovered from mountain reedbuck during the November 1983 to December 1985 survey is graphically illustrated

TABLE 3 The helminths recovered from springbok in the Karoo, Mountain Zebra and West Coast National Parks, and on the farm near Bredasdorp

Locality, number of hosts examined and helminth species	Number of helminths recovered			Prevalence %
	Larvae	Adults	Total	
Mountain Zebra National Park ($n = 2$)				
Cooperioides antidorca	0	1 275	1 275	50
Haemonchus bedfordi	0	475	475	100
Longistrongylus albifrontis	0	89	89	50
Nematodirus spathiger	2 625	1 175	3 800	100
Ostertagia type females	–	25	25	50
Paracooperia serrata	0	1 175	1 175	50
Trichostrongylus falculatus	0	10 975	10 975	100
Mean total burden	1 313	7 595	8 908	
Karoo National Park ($n = 4$)				
Agriostomum equidentatum	0	40	40	25
Bronchonema magna	0	190	190	50
Cooperioides antidorca	0	30	30	25
Paracooperia serrata	0	145	145	75
Nematodirus spathiger	1 481	4 818	6 299	100
Trichostrongylus falculatus	0	996	996	100
Mean total burden	370	1 555	1 925	
West Coast National Park ($n = 2$)				
Bronchonema magna	0	58	58	100
Cooperia rotundispiculum race	0	160	160	50
Cooperioides antidorca	0	83	83	50
Longistrongylus curvispiculum	0	309	309	100
Longistrongylus namaquensis	0	298	298	100
Nematodirus spathiger	0	1 552	1 522	100
Paracooperia serrata	0	662	662	100
Trichostrongylus deflexus	0	905	905	100
Mean total burden	0	2 014	2 014	
The farm near Bredasdorp ($n = 1$)				
Bronchonema magna	–	30	30	100
Haemonchus bedfordi	[a]	60	60	100
Longistrongylus curvispiculum	[a]	3 880	3 880	100
Nematodirus spathiger	[a]	1 520	1 520	100
Ostertagia ostertagi	[a]	600	600	100
Trichostrongylus falculatus	[a]	120	120	100
Total burden	[a]	6 210	6 210	

– Not applicable

[a] Mucosal digests not done

in Fig. 1. With the exception of May 1984, when a peak burden of 1 875 nematodes was recorded, the tri-monthly mean burdens varied from 65–645 nematodes. No worms were recovered from the antelope examined during September 1985.

Trichostrongylus falculatus was the most numerous nematode in springbok, contributing 72 % to the mean adult nematode burden, and together with *Cooperioides antidorca* (8 %), *Nematodirus spathiger* (8 %) and *Paracooperia serrata* (8 %), accounted for 96 % of the burden (Table 3).

Karoo National Park

Neither of the two black wildebeest nor the two mountain reedbuck examined in this park had any worms. One grey rhebuck harboured 50 *Nematodirus spathiger*, 20 of which were fourth stage larvae, while the other harboured only a single *Haemonchus bedfordi* male.

Nematodirus spathiger was the most numerous nematode in springbok, and contributed 77 % to the mean total adult nematode burden, followed by *Trichostrongylus falculatus* with 16 % (Table 3).

TABLE 4 The helminths recovered from two bontebok in the West Coast National Park

Helminth species	Number of helminths recovered			Prevalence %
	Larvae	Adults	Total	
Bronchonema magna	0	44	44	100
Cooperia rotundispiculum race	0	400	400	100
Haemonchus contortus	0	80	80	50
Longistrongylus curvispiculum	a	3 190	3 190	100
Longistrongylus namaquensis	a	170	170	50
Ostertagia type females	–	3 970	3 970	100
Ostertagia type larvae	5 483	–	–	100
Nematodirus spathiger	364	6 277	6 277	100
Teladorsagia circumcincta	a	335	335	100
Trichostrongylus axei	0	82	82	100
Trichostrongylus thomasi	0	230	230	100
Mean total burden	2 924	7 389	10 313	

a Larvae and females indistinguishable at species level and grouped together as *Ostertagia* type
– Not applicable

TABLE 5 The helminths recovered from two gemsbok in the West Coast National Park

Helminth species	Number of helminths recovered			Prevalence %
	Larvae	Adults	Total	
Bronchonema magna	0	10	10	100
Longistrongylus curvispiculum	0	101	101	50
Nematodirus spathiger	600	13 002	13 602	100
Ostertagia ostertagi	0	3 111	3 111	100
Trichostrongylus deflexus	0	345	345	50
Trichostrongylus falculatus	0	1 036	1 036	50
Trichostrongylus pietersei	0	1 781	1 781	100
Trichostrongylus rugatus	0	37 176	37 176	100
Trichostrongylus thomasi	0	219	219	50
Mean total burden	300	28 391	28 691	

West Coast National Park

The helminths collected from bontebok are listed in Table 4. The most abundant adult nematodes in this host were *Nematodirus spathiger,* which contributed 42 % to the mean total adult nematode burden, while the ostertagiid nematodes *Longistrongylus curvispiculum, Longistrongylus namaquensis, Teladorsagia circumcincta* and the *Ostertagia* type females together accounted for 52 %. The remaining nematodes occurred in small numbers.

The only gastro-intestinal nematode in eland from this park was *the Cooperia rotundispiculum* race, which occurred in large numbers (Table 1).

Trichostrongylus rugatus was the most numerous adult nematode in gemsbok (65 %) and together with *Nematodirus spathiger* (23 %), contributed 88 % of the mean total adult nematode population (Table 5).

Nematodirus spathiger accounted for 39 % of the adult nematodes in springbok, *Trichostrongylus deflexus* for 22 % and the remaining nematodes for 39 % (Table 3).

The farm near Bredasdorp

Longistrongylus curvispiculum accounted for 62 % of the adult nematode burden in the springbok, *Nematodirus spathiger* for 24 % and the remaining four nematode species for 14 % (Table 3).

DISCUSSION

Black wildebeest

Although a fairly common antelope species in the colder regions of the country, the helminths of black wildebeest have received little attention. Round (1968) recorded a trematode species, a larval *Taenia* sp. and five nematode species, Young, Zumpt, Boomker, Penzhorn & Erasmus (1973a) a *Haemonchus* sp. and an *Oesophagostomum* sp., and Horak

TABLE 6 The nematode species recovered per host species per locality

Helminth species	Mountain Zebra National Park					Karoo National Park				West Coast National Park				Farm		Number of host species infected
	Connochaetes gnou	*Taurotragus oryx*	*Redunca fulvorufula*	*Pelea capreolus*	*Alcelaphus buselaphus*	*Antidorcas marsupialis*	*Connochaetes gnou*	*Redunca fulvorufula*	*Pelea capreolus*	*Antidorcas marsupialis*	*Damaliscus pygargus dorcas*	*Oryx gazella*	*Taurotragus oryx*	*Antidorcas marsupialis*	*Antidorcas marsupialis*	
Agriostomum equidentatum	–	–	–	–	–	–	–	–	–	+	–	–	–		–	1
Bronchonema magna	–	–	–	–	–	–	–	–	–	+	+	+[a]	+[a]	+	+	4
Cooperia rotundispiculum	–	+	–	–	–	–	–	–	–	–	+[a]	–	+[a]	+[a]	–	3
Cooperioides antidorca	–	–	–	–	–	+	–	–	–	+	–	–	–	+	–	1
Haemonchus sp.	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Haemonchus bedfordi	–	–	–	–	–	+	–	–	+[a]	–	–	–	–	–	+	2
Haemonchus contortus	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	1
Haemonchus mitchelli	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Longistrongylus albifrontis	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	1
Longistrongylus curvispiculum	–	–	–	–	–	–	–	–	–	–	+	+[a]	–	+	+	3
Longistrongylus namaquensis	–	–	–	–	–	–	–	–	–	–	+	–	–	+	–	2
Nematodirus spathiger	–	+[a]	+	–	+[a]	+	–	–	+	+	+	+	–	+	+	7
Ostertagia ostertagi	–	–	–	–	–	–	–	–	–	–	–	+[a]	–	–	+[a]	2
Ostertagia type females	–	–	+	–	–	+	–	–	–	–	+	–	–	–	–	3
Paracooperia serrata	–	–	–	–	–	+	–	–	–	+	–	–	–	+	–	1
Skrjabinema sp.	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	1
Teladorsagia circumcincta	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	1
Trichostrongylus axei	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	1
Trichostrongylus deflexus	–	–	–	–	–	–	–	–	–	–	–	+[a]	–	+	–	2
Trichostrongylus falculatus	–	–	+[a]	–	+[a]	+	–	–	–	+	–	+	–	–	+	4
Trichostrongylus pietersei	–	–	–	–	–	–	–	–	–	–	–	+[a]	–	–	–	1
Trichostrongylus rugatus	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	1
Trichostrongylus thomasi	–	–	–	–	–	–	–	–	–	–	+	+[a]	–	–	–	2
Number of helminth species per host	1	3	4	0	2	7	0	0	2	6	10	9	2	8	6	

[a] New record

et al. (1983) *Haemonchus bedfordi, Oesophagostomum columbianum,* a *Trichuris* sp. and a *Thysaniezia* sp.

The single *Taenia* sp. larva recovered in the black wildebeest in the Mountain Zebra National Park could not be assigned to a species. Gough (1908) and Ortlepp (1961) recorded larval *Taenia hydatigena* in black wildebeest. Horak *et al.* (1983) did not find any larval cestodes in ten black wildebeest from a nature reserve in the Free State and another in Gauteng but found 34,5 % of 55 blue wildebeest, *Connochaetes taurinus,* in the Kruger National Park to be infected with the larval stages of *Taenia regis.*

The nematode burden of the black wildebeest examined in this survey is extremely low when compared with that recorded by Horak *et al.* (1983). This probably is a reflection of the adverse climatic conditions, namely hot summers and cold winters with little rainfall during either season, in both the Mountain Zebra and the Karoo National Parks. In addition, wildebeest's apparent resistance to parasite infections (Horak *et al.* 1983) may also have played a role.

Bontebok

The helminths of bontebok have thus far only been studied in the Bontebok National Park, and Boomker & Horak (1992) summarized the findings of several authors.

The only cestodes that have been recovered from these animals are *Moniezia expansa* (Boomker & Horak 1992) and a single *Taenia hydatigena* larva (Verster, Imes & Smit 1975). No cestodes were recovered from the two bontebok in the West Coast National Park.

We assume that a *Cooperia rotundispiculum* race, typical *Haemonchus contortus, Teladorsagia circumcincta* and *Trichostrongylus thomasi* were acquired from other antelope, especially springbok and eland or gemsbok, in the West Coast National Park since they did not occur in the Bontebok National Park. *Cooperia rotundispiculum* is a new parasite record for bontebok.

The mean adult nematode burden of bontebok surveyed in the Bontebok National Park during 1975, 1976 and 1979 was 6 787 (Horak, Brown, Boomker, De Vos & Van Zyl 1982b), while the mean adult nematode burden was 5 661 in the survey conducted during 1983–1984 (Boomker & Horak 1992). The bontebok from the West Coast National Park harboured a mean of 10 313 adult nematodes. We believe that the larger burden is due to the climatic conditions, the West Coast National Park being further in the winter rainfall region than the Bontebok Park, and the number of other host species present in this park.

Eland

Eland have also not to any significant degree been subject to parasite surveys in recent years. Round (1968) lists only one cestode and five nematode species from this host, and Mares, Amaral & Fachada (1984) two cestode genera and a nematode species from two eland in the former Republic of Transkei, now part of the Eastern Cape Province.

Nematodirus spathiger, Bronchonema magna and a race of *Cooperia rotundispiculum* constitute new parasite records for eland. *Bronchonema magna* was in all probability acquired from the springbok, which is the preferred host, while the other two species could have been acquired from any of the other antelopes present in the reserves.

Mares *et al.* (1984) do not record the actual numbers of nematodes recovered from the eland they examined and no other records of helminth burdens in eland could be found. The eland from the West Coast National Park harboured about eight times the mean number of nematodes of those in the Mountain Zebra National Park. We presume that these differences are largely due to the climate and stocking rates.

Grey rhebuck

As with the bontebok, the helminths of grey rhebuck have only been studied in the Bontebok National Park, and Boomker & Horak (1992) have summarized the findings of several authors.

Haemonchus bedfordi is a new parasite record for grey rhebuck and, as only one nematode was found in one of the antelope, it should be considered an accidental parasite.

The helminth burdens of these antelope in the Karoo National Park are insignificant and no comparison with the burdens of the antelope from the Bontebok National Park is possible.

Gemsbok

Although gemsbok are common in the more arid areas of South Africa, and are popular antelope with game farmers and hunters, few helminth surveys have been conducted on them. Round (1968) lists larval *Taenia hydatigena,* a cestode species and four nematode species as occurring in gemsbok in South Africa. Mares *et al.* (1984) list *Fasciola hepatica* and *Haemonchus contortus* from three antelope in the then Republic of Transkei. Gemsbok in the National Kalahari Gemsbok Park harboured *Agriostomum equidentatum, Haemonchus contortus, Longistrongylus meyeri, Paracooperia serrata, Impalaia nudicollis* and *Strongyloides* sp., all of which are parasites more commonly encountered in springbok (Boomker, Horak & De Vos 1986). Fourie, Vrahimis, Horak, Terblanche & Kok (1991) recorded a cestode genus and the larvae of *Taenia* spp., as well as the larval stages of two nematode genera, the adults of four nematode genera and 13 nematode species from gemsbok introduced into the Willem Pretorius Nature Reserve in the Free State.

In the West Coast National Park, the gemsbok harboured a large variety of nematodes. Of these, *Nematodirus spathiger* and *Trichostrongylus rugatus* should be considered as definitive parasites, while *Ostertagia ostertagi, Trichostrongylus falculatus* and *Trichostrongylus pietersei* are occasional parasites. *Longistrongylus curvispiculum* and *Trichostrongylus deflexus* should be regarded as accidental parasites since they occurred in small numbers in only one of the gemsbok. New parasite records for gemsbok are *Bronchonema magna, Longistrongylus curvispiculum, Ostertagia ostertagi, Trichostrongylus deflexus, Trichostrongylus pietersei* and *Trichostrongylus thomasi.*

The gemsbok from the Kalahari National Gemsbok Park harboured 5 877 intestinal helminths (Boomker *et al.* 1986), those from the Willem Pretorius Nature Reserve a mean of 1 497 (Fourie *et al.* 1991) and those from the West Coast National Park a mean of 28 681 intestinal nematodes. We are of the opinion that the large burdens of the last named antelope are mainly due to climatic conditions and stocking rates.

Mountain reedbuck

The helminths of mountain reedbuck are also not well known despite this antelope's relative abundance in southern Africa.

Gough (1908) records a *Taenia* sp. larva, Veglia (1919*) Paramphistomum bothriophoron, Paramphistomum cervi* and *Haemonchus contortus,* Thwaite (1927) *Setaria boulengeri,* and Mönnig (1924) *Setaria hornbyi.* Ortlepp (1961) mentions only *Setaria boulengeri* and Baker & Boomker (1973) recovered ten nematode species, three nematode genera, *Paramphistomum* spp. (*sic*) and the larval stages of *Taenia* spp. from mountain reedbuck in the Loskop Dam Nature Reserve in the then Transvaal (now Mpumalanga). In addition, Baker & Boomker (1973) and Young *et al.* (1973a) found *Haemonchus* sp., *Nematodirus spathiger, Setaria boulengeri* and *Moniezia expansa* from these antelope in the Mountain Zebra National Park.

Moniezia benedeni and *Trichostrongylus falculatus* are new parasite records for mountain reedbuck.

Baker & Boomker (1973) recorded 1 107 nematodes from the small intestine of mountain reedbuck shot in the Loskop Dam Nature Reserve. Young *et al.* (1973a) did not record the numbers of helminths recovered from mountain reedbuck from the Mountain Zebra National Park but the mean adult nematode burden of the antelope from the same locality examined in this study was 283, which is negligible.

Comment: The identifications of *Paramphistomum* spp. in these antelope should be treated with reserve. According to Eduardo (1983), the genus *Paramphistomum* in Africa is limited to *Paramphistomum cephalophi,* from *Cephalophus nigrifrons* in Rwanda. *Paramphistomum bothriophoron* has been transferred to the genus *Calicophoron* (Eduardo 1983) while *Paramphistomum cervi* is in all probability a misidentification.

Red hartebeest

As with the gemsbok, red hartebeest are antelope that prefer the drier parts of the country. Few helminths have been recorded from these animals, and Ortlepp (1961) lists two trematode and five nematode species. Mares *et al.* (1984) added two cestode genera, three nematode genera and two nematode species, while Boomker *et al.* (1986) added *Impalaia nudicollis* and a *Parabronema* sp. to the list. *Nematodirus spathiger* and *Trichostrongylus falculatus* are new parasite records for these antelope.

Boomker *et al.* (1986) found 1 774 helminths in the red hartebeest from the Kalahari Gemsbok National Park, which is comparable to the 1 825 recorded from these antelope from the Mountain Zebra National Park.

Springbok

The helminths of springbok have been well documented by Ortlepp (1961), Round (1968), Young, Zumpt, Basson, Erasmus, Boyazoglu & Boomker (1973b), Horak, Meltzer & De Vos (1982a), De Vos (1982a), De Villiers, Liversidge & Reinecke (1985) and Boomker *et al.* (1986). A cestode genus, a cestode species and two larval cestodes, one trematode species, and 27 nematode species and four nematode genera have thus far been recovered.

De Villiers *et al.* (1985) recorded helminth burdens ranging from 2 954–12 224 in springbok from the Northern Cape Province. Horak *et al.* (1982a) found springbok in the Bontebok National Park to harbour 7 129–17 819 nematodes, those from Gauteng 2 563–11 585, and those from the Northwest Province 12 449–71 790. The numbers of fourth stage larvae often exceeded those of the adults nematodes. In the surveys conducted by De Villiers *et al.* (1985) and Horak *et al.* (1982), *Paracooperia serrata* was the most common nematode. The springbok from the Karoo and West Coast National Parks had insignificant numbers of this helminth and *Nematodirus spathiger* was the most commonly encountered parasite in both parks.

Ostertagia ostertagi from the antelope from the farm near Bredasdorp and *Cooperia rotundispiculum* from the antelope in the West Coast National Park are new parasite records for springbok.

A summary of the host associations and the number of helminth species per host per locality are presented in Table 6. From this table it is apparent that bontebok in the West Coast National Park harboured the greatest number of nematode species (ten) followed by gemsbok (nine) and springbok (eight) at the same locality. Springbok in the Mountain Zebra National Park had seven species of nematodes and these antelope in the Karoo National Park and on the farm near Bredasdorp had six species. We believe that the number of antelope species in the West Coast National Park influenced the variety and the numbers of the helminths recovered from them.

Helminths

Although *Bronchonema magna* was originally described from blesbok, *Damaliscus pygargus phillipsi* by Mönnig (1932), it seems to be equally common in springbok (Ortlepp 1962) and bontebok (Verster *et al.* 1975; Horak *et al.* 1982b). However, it seems springbok are the preferred host of these nematodes and they tend to disappear from other antelope when springbok are removed from an area, as discussed by Boomker & Horak (1992). Since the nematodes occurred only in springbok in the Karoo National Park, but in all four the antelope species in the West Coast National Park, we believe that the presence of springbok in the West Coast National Park is undesirable.

Nematodirus spathiger is well-adapted to the semi-arid regions (Viljoen 1969). Since the infective third stage larvae occur within the egg and only hatch after good rain, massive infections are possible (Reinecke 1983). It appears to be a definitive parasite of all the hosts examined in this survey. As is evident from Table 5, gemsbok in the West Coast National Park seem to be especially good hosts.

Both *Trichostrongylus axei* and *Trichostronglylus thomasi* were recovered from the abomasum of both the bontebok in the West Coast National Park. The latter nematode represents a new parasite record for bontebok and usually fills the niche in antelope that *Trichostrongylus axei* occupies in domestic ruminants. Previous records of *T. thomasi* are from animals in the Kruger National Park and its surrounds, Mpumalanga (Horak *et al.* 1983; Boomker *et al.* 1989b), impala and red duiker in north-eastern KwaZulu-Natal (Boomker, Horak, Flamand & Keep 1989a; Boomker, Horak & Flamand 1991b), springbok near Lichtenburg, Northwest Province (Horak *et al.* 1982a) and kudu in the Etosha Game Reserve, Namibia (Boomker, Anthonissen & Horak 1988). All these localities are more than 1 000 km north of the West Coast National Park and it seems likely that this nematode was introduced into this park with one of the host species, probably gemsbok.

Trichostrongylus rugatus is a common parasite of domestic sheep and goats in the southern Eastern and Western Cape Province (Boomker *et al.* 1989c; Horak, Knight & Williams 1991; Reinecke, Kirkpatrick, Swart, Kriel & Frank 1987) and appears to be equally well adapted to gemsbok.

CONCLUSION

The danger of translocating antelope to small game reserves without prior anti-parasitic treatment has been pointed out by Horak (1980). Similarly, the translocation of antelope to climatic or vegetation regions where they normally did not occur can also be dangerous. We believe that a potentially hazardous situation exists in the West Coast National Park, where the climatic conditions appear to be favourable for the worms but cause stress especially in gemsbok and bontebok. For example, gemsbok in the Kalahari Gemsbok National Park harboured a total of 5 877 nematodes, including fourth stage larvae (Boomker *et al.* 1986), while those in the Free State harboured approximately 2 866 (Fourie *et al.* 1991). The mean burden of the antelope in the West Coast National Park was 28 691, which is 4,9–10 times as many worms.

A similar situation occurred in bontebok when they were kept near the town of Bredasdorp. They did not grow or reproduce well and harboured large numbers of parasites (Van der Walt & Ortlepp 1960). They were then moved to the current locality, near Swellendam, where their numbers increased and, presumably, their parasite loads declined.

As far as the helminths are concerned, a similar situation seems to develop in the West Coast National Park. Antelope in the Bontebok National Park harboured a mean of 1 722 adult trichostrongylids during the 1979 survey (Horak *et al.* 1982b) and 5 382 during the 1983/84 survey (Boomker & Horak 1992), *Nematodirus spathiger* being the most common nematode in both surveys. The mean number of adult helminths in the two bontebok in this survey was 7 389, the majority of which were ostertagiid nematodes of the genus *Longistrongylus.* The latter nematode genus is considered more pathogenic than *Nematodirus,* since they occur in the abomasum where they cause lesions similar to those of *Ostertagia* spp. and *Teladorsagia* spp. of cattle and sheep (Pletcher, Horak, De Vos & Boomker 1984). In addition, the forced association of antelope lends itself to cross infection. The occurrence of *Bronchonema* in gemsbok and eland can only be ascribed to the presence of springbok, while *Cooperia rotundispiculum* in springbok, eland and bontebok is the direct result of sharing pastures with eland. The *Cooperia* spp. are generally considered harmless in well-fed adult animals (Reinecke 1983), but *Bronchonema* may in time cause the death of some of the antelope.

ACKNOWLEDGEMENTS

We thank the Board of Trustees, South African National Parks, for making the antelope available to us, the staff of the various National Parks for their valued and excellent assistance with processing the animals and Mr Mick Dalton, owner of the farm near Bredasdorp for making the springbok available. This work was done with the partial financial assistance of the Foundation for Research Development (now the National Research Foundation).

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J. Parasitol., 91(4), 2005, pp. 863–870
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HELMINTHS IN SYMPATRIC POPULATIONS OF MOUNTAIN REEDBUCK (*REDUNCA FULVORUFULA*) AND GRAY RHEBOK (*PELEA CAPREOLUS*) IN SOUTH AFRICA

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ABSTRACT: Helminths of mountain reedbuck (*Redunca fulvorufula fulvorufula*) and gray rhebok (*Pelea capreolus*) were investigated in South Africa between June 1999 and February 2002. Forty-one mountain reedbuck were culled at Sterkfontein Dam Nature Reserve over 8 different periods, and 25 mountain reedbuck were culled at Tussen die Riviere Nature Reserve over 3 different periods. A total of 17 kinds of helminths were found at the 2 sites, including 15 nematodes, 1 trematode, and 1 cestode. At Sterkfontein, the most prevalent and abundant species were *Cooperia yoshidai*, *Longistrongylus schrenki*, and *Haemonchus contortus*, with the latter 2 being more abundant during November/December than at other times of the year, probably because infective larvae increased on pasture at that time. No statistical differences were found in parasite loads between male and female mountain reedbuck. No correlation was found between fecal egg counts and adult worm counts or between parasite counts and body condition. At Tussen die Riviere, helminths in mountain reedbuck were less prevalent and abundant than at Sterkfontein. The most important species were *Nematodirus spathiger*, *Trichostrongylus falculatus*, and *Cooperia rotundispiculum*. Four gray rhebok died of natural causes at Sterkfontein, from which 5 kinds of helminths were recovered, including *C. yoshidai* and *Paracooperioides peleae*.

Southern mountain reedbuck (*Redunca fulvorufula fulvorufula*) and gray rhebok (*Pelea capreolus*) use rocky hillsides, steep grasslands, and mountain slopes that form marginal habitat for most other ungulate species in South Africa (Skinner and Smithers, 1990). In many areas, they are sympatric but maintain separate ecological niches in feeding and social habits. Mountain reedbucks are selective grazers and have social structures, including solitary and territorial males, unstable female herds with young, and bachelor groups (Irby, 1979; Dunbar and Roberts, 1992). Gray rhebok are browsers, feed mostly on forbs (Beukes, 1984; Ferreira and Bigalke, 1987), and form stable harem herds in which a dominant male permanently maintains a small group of females and young. Males without territories remain solitary (Esser, 1973; Ferreira and Bigalke, 1987).

The present study formed part of a wider project investigating factors influencing productivity in the 2 species. Mountain reedbuck have the potential to be cropped for meat production. They are fecund; produce good-quality, edible meat; and because they use marginal habitat, do not generally compete with other grazers (Irby, 1979; Skinner, 1980). Gray rhebok are less likely candidates for commercial meat production, because they are less common, are difficult to hunt, and are not favored for consumption (Skinner and Smithers, 1990). They are, however, highly marketable for trophy hunting.

Numerous fitness traits may be negatively affected by parasitic infections, including productivity (Wilson et al., 2002). The degree to which parasite effects translate into changes to host populations likely will depend on many factors, including dispersion of parasites among hosts, magnitude of parasite effects, and degree to which ages and sexes differ in parasitism (Schalk and Forbes, 1997).

The parasites of mountain reedbuck are not well known, despite the relative abundance of these antelopes in South Africa (Boomker et al., 2000). Baker and Boomker (1973) found 17 helminth species (14 nematodes, 2 cestodes, and 1 trematode) in mountain reedbuck at 2 sites within South Africa, but to our knowledge, no seasonal or gender differences have been investigated. The parasites of gray rhebok are even less well known (Boomker et al., 2000), with 12 nematode and 1 trematode species being found at a single site (Boomker et al., 1981; Horak et al., 1982).

The aim of the present study was to identify and quantify helminths of mountain reedbuck and gray rhebok as well as to investigate effects of season, host age, and host gender on the occurrence and numbers of parasites. Because helminths from both antelopes are poorly known, the present study provides additional helminthological data from new localities.

MATERIALS AND METHODS

Study sites

The present study was conducted at 2 Provincial Nature Reserves within the Free State Province of South Africa. Sterkfontein Dam Nature Reserve (hereafter Sterkfontein; 28°24′S, 29°02′E) has a total land area of 11,000 ha and an altitude varying between 1,700 and 2,350 m. It has a mild climate, with an average temperature of 17 C and average summer rainfall of 680 mm. Occasional snow and frequent burning have a major influence on the vegetation. Sterkfontein falls mainly within the Moist Cool Highveld Grassland (Bredenkamp and van Rooyen, 1996) and, in pristine condition, is dominated by the grass *Themeda triandra*.

Tussen die Riviere Nature Reserve (hereafter TdR; 30°30′S, 26°07′E) has an area of 22,000 ha, with an altitude varying between 1,200 and 1,500 m. Mean temperatures are 18 C, and annual summer rainfall averages 420 mm. The TdR falls in the Eastern Mixed Nama Karoo (Hoffman, 1996) and has a complex mix of grass- and shrub-dominated vegetation types.

Study animals

Culling schedules of mountain reedbuck differed between the 2 sites as a result of differing management programs. At Sterkfontein, 41 animals were culled over a 2-yr period. Eight separate culls were carried out at 3-mo intervals, with approximately 5 animals culled during each of the following months: March, June, September, and December 2000; May, August, and November 2001; and February 2002. In a typical culling period, 2 adult males, 2 adult females, and 1 juvenile of either sex were selected without knowledge of their age (aside from adult/juvenile status) and body condition. In addition to parasite extraction, the approximate age of each animal was estimated using body mass and dentition. Female reproductive condition also was established, and the body condition of each animal was determined using the kidney fat index (KFI), where KFI = (kidney fat wt/kidney wt)·100 (Riney, 1955).

Received 20 July 2004; revised 28 October 2004; accepted 1 November 2004.

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TABLE I. Prevalence and abundance of helminths recovered from 41 mountain reedbuck culled at Sterkfontein Dam Nature Reserve between March 2000 and February 2002.*

Nematode genera and some species	Prev. (%)	Site in host	Mean (n)	SD (n)	Range (n)
Calicophoron sp. (T)	5	Rum	6.1	27.8	0–150
Haemonchus sp. L4 (N)	32	Abo	21.4	61.9	0–350
Haemonchus contortus (N)	66	Abo	115.8	218.2	0–1,050
Longistrongylus sp. L4 (N)	44	Abo	72.9	135.0	0–470
Longistrongylus schrenki (N)‡	80	Abo	36.5	56.8	0–230
Longistrongylus namaquensis (N)‡	2	Abo	0.2	1.6	0–10
Ostertagia sp. (N)‡	2	Abo	0.2	1.6	0–10
Cooperia sp. L4 (N)	66	SI	312.3	682.3	0–4,050
Cooperia yoshidai (N)	98	SI	2,037.5	2,594.2	0–14,880
Cooperia pigachei (N)†	2	SI	3.7	23.4	0–150
Trichostrongylus falculatus (N)	12	SI	5.4	26.7	0–170
Trichostrongylus deflexus (N)‡	2	SI	0.2	1.6	0–10
Impalaia nudicollis (N)‡	2	SI	0.5	3.1	0–20
Paracooperioides peleae (N)‡	2	SI	0.2	1.6	0–10
Skrjabinema sp. (N)	39	LI	187.9	1,140.4	0–7,310
Moniezia sp. (C)	5	SI	0.1	2.0	0–10

* Prev., prevalence; SD, standard deviation; T, trematode; N, nematode; C, cestode; L4, fourth larval stage; Rum, rumen; Abo, abomasum; SI, small intestine; LI, large intestine.
† New species.
‡ New parasite record.

At TdR, 25 mountain reedbucks were culled over 3 separate time periods: December 1999, June 2000, and June 2001. Most of the animals were culled at night using spotlights and, therefore, were selected randomly. Approximate age, reproductive status, and KFI were determined.

Gray rhebok were not culled for meat production, and although they are occasionally used for trophy hunting, no systematic removal occurred during the present study. Therefore, parasite collection was only carried out from 4 animals that died naturally at Sterkfontein and, as a result, was only useful for limited helminth species identification.

Recovery of alimentary helminths

Rumens were opened and examined for paramphistomes. Parasites of the abomasa, small intestines, large intestines (including ceca), lungs, liver, and heart were collected as described by Horak (1978c). Aliquots representing one-tenth of the volume of each ingesta were collected for microscopic examination and stored in 70% ethanol. Species were identified using species descriptions (Boomker, 1977, 1991; Boomker et al., 1981; Gibbons, 1981; Boomker and Reinecke, 1989). Male nematodes were identified to the species level, and in most cases, females also could be identified to the species level by extrapolation. For cases in which male nematodes were not present, females were identified to the genus level only. Trematodes and cestodes were identified to the generic level only.

TABLE II. Prevalence and abundance of helminths recovered from 25 mountain reedbuck at Tussen die Riviere Nature Reserve between December 1999 and June 2001.*

Nematode genera some species	Prev. (%)	Site in host	Mean (n)	SD (n)	Range (n)
Calicophoron sp. (T)	4	Rum	2.0	12.5	0–80
Haemonchus contortus (N)	28	Abo	4.0	10.2	0–50
Longistrongylus albifrontis (N)	8	Abo	0.3	2.1	0–10
Nematodirus spathiger (N)	58	SI	15.1	22.5	0–100
Trichostrongylus falculatus (N)	31	SI	29.6	70.0	0–240
Cooperia rotundispiculum (N)†	31	SI	19.3	64.2	0–320
Cooperia yoshidai (N)	4	SI	0.4	2.0	0–10
Impalaia nudicollis (N)†	8	SI	1.7	6.0	0–30
Skrjabinema sp. (N)	4	LI	0.4	2.0	0–10
Setaria sp. (N)	4	Vis	0.1	0.2	0–1
Moniezia sp. (C)	4	SI	0.4	2.0	0–10

* Prev., prevalence; SD, standard deviation; T, trematode; N, nematode; C, cestode; Rum, rumen; Abo, abomasum; SI, small intestine; LI, large intestine; Vis, visceral cavity.
† New parasite record.

Fecal egg counts and larval culture

Feces were collected from 18 culled mountain reedbuck and from live gray rhebok at Sterkfontein. From the latter, feces were collected fresh off the ground twice a month from 5 animals between September 2001 and April 2002. Egg counts were carried out using the McMaster method (Reinecke, 1983) ("Eggs-Acto" McMaster egg counting chamber; Focal Point, Pretoria, South Africa; http://www.mcmaster.co.za), but no attempt was made to identify species. The remaining feces were used to culture larvae (Reinecke, 1983), which were harvested and counted after 10 and 14 days from each sample.

Statistical methods

Two-way ANOVAs were used to test for differences in parasite burdens in mountain reedbuck between genders and months. As with most parasite population data, the nematodes were strongly aggregated, so the data had to be $\log_{10}$ transformed. Because the occurrence of 1 species of nematode in the GIT was not dependent on or affected by the occurrence of another species, it was not of interest to test for differences between nematode species. Therefore, 3 separate 2-way ANOVAs were carried out for the 3 main nematode species. One-way ANOVA and Kruskal–Wallis ANOVA on ranks were used to test for differences in parasite loads of animals of different ages and females with varying degrees of pregnancy. Spearman rank-correlation coefficients were used to determine whether a correlation existed between the number of nematodes extracted and the KFI of each animal and to compare fecal egg counts with cultured larvae counts and adult worm counts.

RESULTS

Helminth species prevalence and abundance

Seventeen kinds of helminths, including 15 nematodes, 1 trematode, and 1 cestode, were recovered from mountain reedbuck at Sterkfontein and TdR (Tables I, II). At Sterkfontein, a

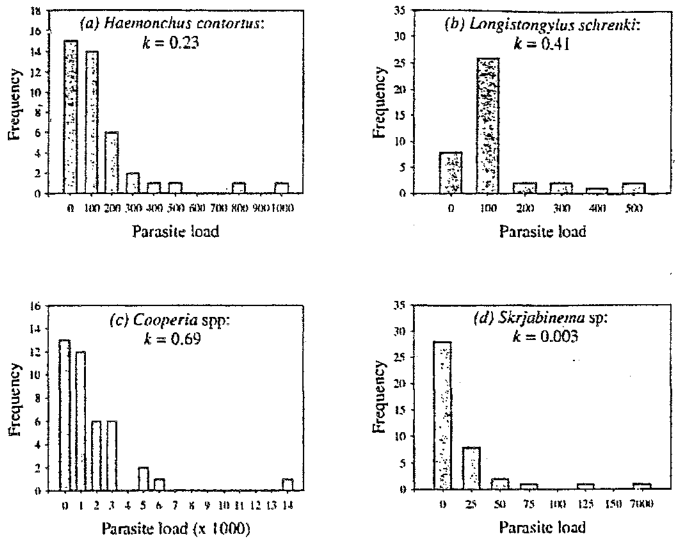

FIGURE 1. Observed frequency distributions of (a) *Haemonchus contortus*, (b) *Longistrongylus schrenki*, (c) *Cooperia* spp., and (d) *Skrjabinema* sp. found in 41 mountain reedbuck culled at Sterkfontein Dam Nature Reserve between March 2000 and February 2002. *k*, corrected moment estimate for aggregation.

new species of *Cooperia*, *Cooperia pigachei*, was found (Boomker and Taylor, 2004), and 6 new parasite records were established. At TdR, 2 new parasite records were established, and nematodes were less prevalent and abundant than at Sterkfontein.

Frequency distributions of nematodes at Sterkfontein

Figure 1 shows the frequency distributions of the 4 most common nematode species found in mountain reedbuck at Sterkfontein. All were highly aggregated. The degree of aggregation was tested using the corrected-moment estimate of k (Wilson et al., 2002):

$$k = (m^2 - s^2/n)/(s^2 - m)$$

where m = mean, s^2 = variance, and n = sample size.

Abomasum nematodes at Sterkfontein

Figure 2 shows seasonal variation in *Haemonchus contortus* and *Longistrongylus schrenki*. Differences between genders and between months (not seasons) in the numbers of *H. contortus* were tested for using a 2-way ANOVA. We found strong evidence for a difference in the number of parasites between months (ANOVA: $F = 5.352$, df = 7, $P < 0.001$), but we found no evidence for a difference between males and females (ANOVA: $F = 0.365$, df = 1, $P = 0.551$). Multiple pairwise comparisons using the Tukey test indicated that numbers of *H. contortus* were higher in December than in May, June, August, and September. We found marginal evidence for an interaction (ANOVA: $F = 2.044$, df = 7, $P = 0.089$). Males had more *H. contortus* than females in the autumn and winter, whereas females had more *H. contortus* than males in the spring and summer.

For *L. schrenki*, differences between genders and between months also were tested using a 2-way ANOVA. We found some evidence for a difference between months (ANOVA: $F = 2.464$, df = 7, $P = 0.045$), but we found no evidence for a difference between genders (ANOVA: $F = 0.025$, df = 1, $P = 0.875$) and no interaction (ANOVA: $F = 1.405$, df = 7, $P = 0.247$). Multiple pairwise comparisons using the Tukey test indicated that numbers of *L. schrenki* were higher in females in December than in February.

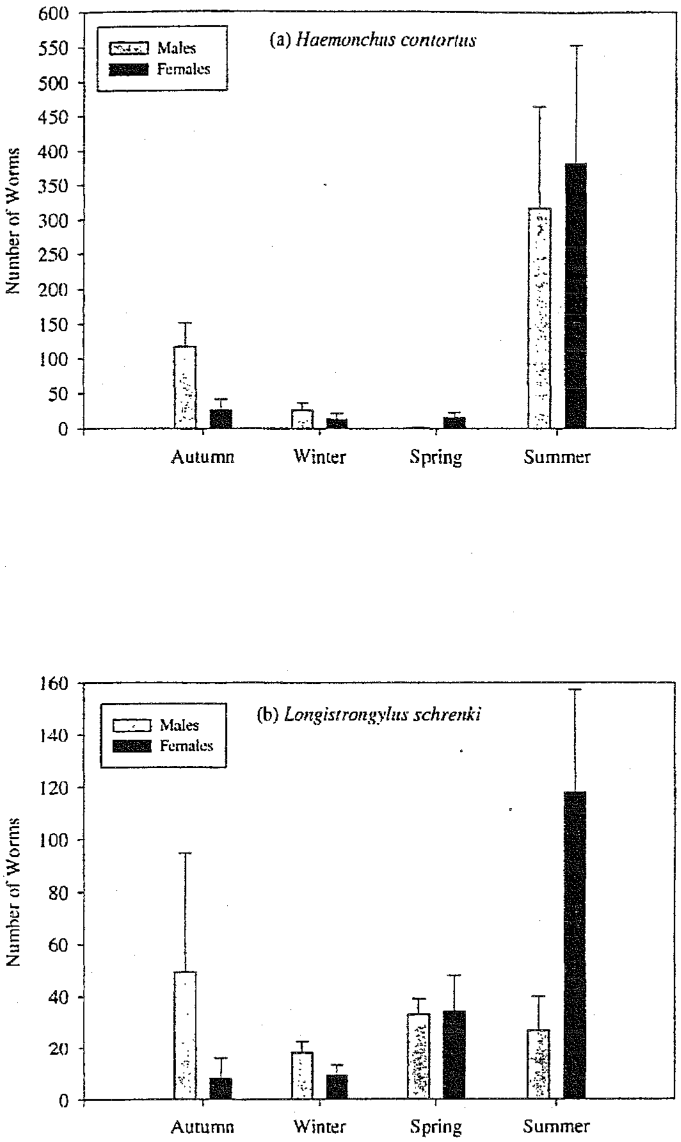

FIGURE 2. Seasonal variation in (a) *Haemonchus contortus* and (b) *Longistrongylus schrenki* in the abomasums of 20 male and 21 female mountain reedbuck at Sterkfontein Dam Nature Reserve. Numbers of animals per gender and per season varied between 4 and 6 (mean = 5). Error bars represent the standard error. Autumn, February/March; winter, May/June; spring, August/September; summer, November/December.

Small intestine nematodes at Sterkfontein

Seasonal variations in *Cooperia* spp. are shown in Figure 3. A 2-way ANOVA comparing variation in numbers of *Cooperia* spp. found no evidence for any differences between genders (ANOVA: $F = 0.050$, df = 1, $P = 0.825$) or between months (ANOVA: $F = 0.435$, df = 7, $P = 0.871$).

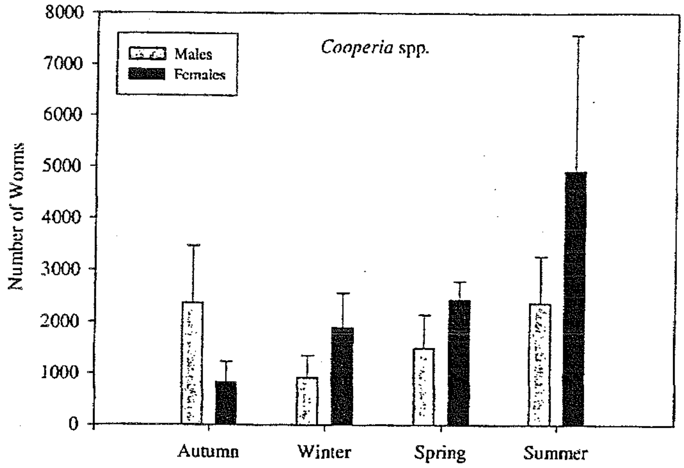

FIGURE 3. Seasonal variation in *Cooperia* spp. in the small intestines of 20 male and 21 female mountain reedbuck at Sterkfontein Dam Nature Reserve. Numbers of animals per gender per season varied between 4 and 6 (mean = 5). Error bars represent the standard error. Autumn, February/March; winter, May/June; spring, August/September; summer, November/December.

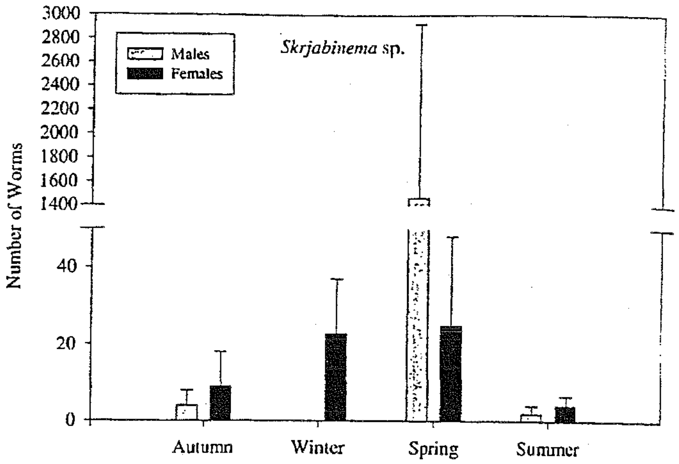

FIGURE 4. Seasonal variation in *Skrjabinema* sp. in the large intestines of 20 male and 21 female mountain reedbuck at Sterkfontein Dam Nature Reserve. Numbers of animals per gender per season varied between 4 and 6 (mean = 5). Error bars represent the standard error. Autumn, February/March; winter, May/June; spring, August/September; summer, November/December.

Large intestine nematodes at Sterkfontein

Skrjabinema sp. occurred at very low numbers in mountain reedbuck at Sterkfontein (Fig. 4). The relatively very large numbers of worms found in males during the spring compared to the other seasons resulted from the occurrence of a large number of worms in only 1 animal. No statistical analysis of differences between genders and between months was attempted.

Age differences

Analysis of the effect of age on parasite distributions in mountain reedbuck at Sterkfontein was limited, because only a small number of young and old animals were sampled. For mountain reedbuck, variation in abundance of *H. contortus* and *Cooperia* spp. were tested for in 3 different age classes. These included animals less than 25 kg (juveniles), animals between 25 and 30 kg (young adults), and animals greater than 30 kg (adults > 2.5 yr). Data for males and females were pooled, both because no statistical differences were found between them and because the sample size was too small to keep them separate. We found no evidence for any differences between the age groups for either *H. contortus* ($H = 1.695$, df = 2, $P = 0.429$) or *Cooperia* spp. ($H = 2.426$, df = 2, $P = 0.297$).

Host body condition

We determined the KFI for each culled mountain reedbuck at Sterkfontein and compared these values with the numbers of nematodes harbored by each animal in the abomasums, small intestines, and large intestines (Fig. 5). A Spearman rank-correlation coefficient found no evidence for a correlation between the numbers of parasites in either the abomasum or small intestine with KFI (abomasum: $r = -0.13$, $P = 0.435$; small intestine: $r = 0.03$, $P = 0.843$). The large intestine was not tested.

Nematodes and pregnancy

Variation in the number of nematodes found in females at varying stages of pregnancy was tested. Comparisons were made between nonpregnant females, pregnant females within the first half of gestation, pregnant females within the second half of gestation, and females that had recently given birth. Stage of pregnancy was estimated from fetal mass using the Hugget and Widdas (1951) formula.

We found evidence for a difference in the number of *H. contortus* between females at different times of pregnancy (ANOVA: $F = 5.11$, df = 3, $P = 0.011$), with females that had recently given birth having more worms than pregnant females within both the first and second halves of pregnancy. We found no evidence for a difference in the number of *Cooperia* spp.

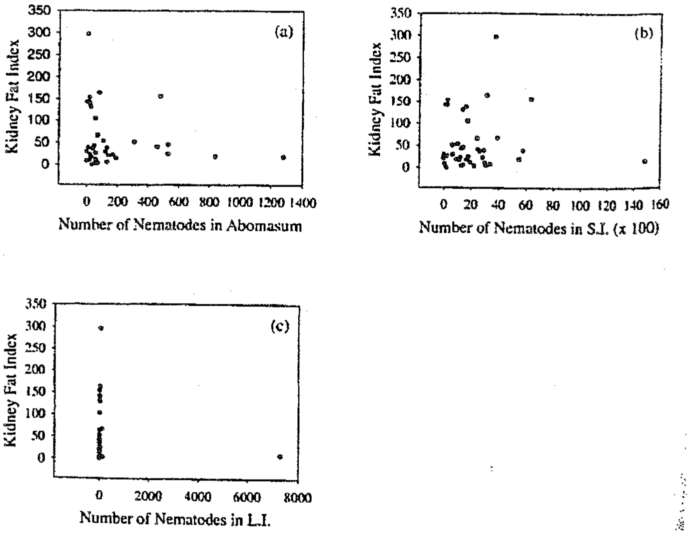

FIGURE 5. Scatter plots of kidney fat index against (a) number of nematodes in the abomasum, (b) number of nematodes in the small intestine, and (c) number of nematodes in the small intestine.

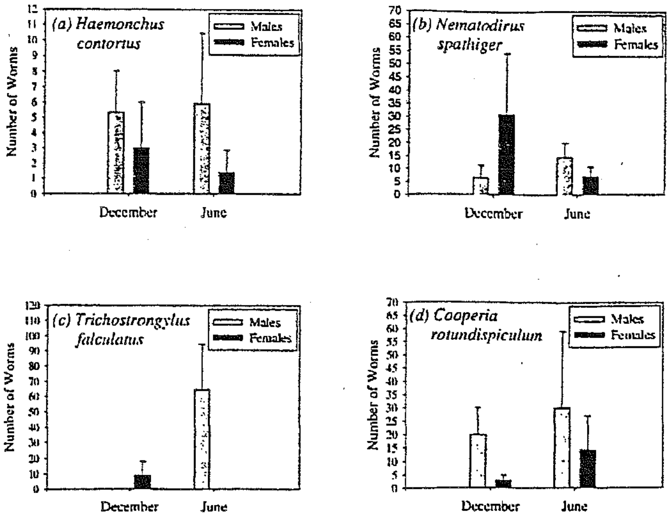

FIGURE 6. Seasonal variation in (**a**) *Haemonchus contortus*, (**b**) *Trichostrongylus falculatus*, (**c**) *Nematodirus spathiger*, and (**d**) *Cooperia rotundispiculum* in 14 male and 11 female mountain reedbuck at Tussen die Riviere Nature Reserve in 1 summer (December 1999) and 2 winter (June 2000 and June 2001) periods. Error bars represent the standard error.

between females at different times of pregnancy (ANOVA: $F = 0.780$, df $= 3$, $P = 0.522$).

Nematodes at TdR

Figure 6 shows the seasonal variation in numbers of the 4 most common species of nematode in mountain reedbuck at TdR between December 1999 and June 2001. Because of their low prevalence and abundance as well as the lack of any apparent pattern in variation between genders and seasons, we saw no reason to test the data statistically.

Nematodes of gray rhebok at Sterkfontein

Five nematode species were extracted from 4 gray rhebok that died at Sterkfontein during 2001 (Table III). Because of the small sample size, no gender or seasonal comparisons were attempted.

Fecal egg counts and larval culture

Fecal egg counts, larval culture counts, and adult worm counts in the GIT from 18 culled mountain reedbuck from Sterkfontein were compared using a Spearman rank-correlation coefficient. Egg counts were highly positively correlated with larval counts ($r_s = 0.952$, n = 18, $P < 0.001$), but we found no correlation between egg counts and adult worms ($r_s = -0.173$, n = 18, $P < 0.565$) or between larval counts and adult worms ($r_s = -0.211$, n = 18, $P < 0.409$).

Fecal egg counts and larval culture counts from gray rhebok were compared using a Spearman rank-correlation coefficient. We found a strong positive correlation between the 2 sampling techniques ($r_s = 0.747$, n = 57, $P < 0.001$). The average number of larvae cultured from 100 g of mountain reedbuck feces was 223,187, compared to 7,702 in gray rhebok.

TABLE III. Prevalence and abundance of nematodes recovered from 4 gray rhebok at Sterkfontein Dam Nature Reserve in 2001.*

Nematode species	Prev. (%)	Site in host	Mean (n)	SD (n)	Range (n)
Haemonchus contortus	50	Abo	32.5	42.7	0–90
Longistrongylus schrenki	25	Abo	15.0	30.0	0–60
Ostertagia sp.	75	Abo	168.8	243.3	0–520
Cooperia yashida†	100	SI	145.0	97.5	10–230
Paracooperioides peleae	50	SI	213.2	282.2	0–590

* Prev., prevalence; SD, standard deviation; Abo, abomasum; SI, small intestine.
† New parasite record.

DISCUSSION

Species prevalence and abundance

The number of helminths found in mountain reedbuck at Sterkfontein and TdR was the same as the number (n = 17) found at 2 other sites within South Africa (Baker and Boomker, 1973). However, 7 of the 14 nematode species found were new parasite records, emphasizing the fact that nematodes of mountain reedbuck are poorly known. Genera of helminths found at Loskop Dam Nature Reserve (Mpumalanga, South Africa) and Mountain Zebra National Park (Eastern Cape, South Africa), but not in the present study, were the nematodes *Gongylonema* sp. and *Oesophagostomum* sp.

Frequency distributions of nematodes

The nematode populations in mountain reedbuck at both Sterkfontein and TdR were highly aggregated, so the majority of the parasite population was concentrated into a minority of the host population. A relatively small number of individuals in the "tail" of the parasite distribution were then responsible for most parasite transmission (Wilson et al., 2002).

Heterogeneities in parasite loads occur in most natural populations (Shaw and Dobson, 1995; Wilson et al., 2002), and these could have a differential effect on host-species fitness and, ultimately, population dynamics. However, it is difficult to tell whether parasite loads, as in the most heavily infected individuals at Sterkfontein, were large enough to have a negative impact. Little information regarding the numbers of nematodes necessary to produce clinical disease in antelope is available (Boomker, 1990).

Pathogenesis caused by *H. contortus* is essentially an acute hemorrhagic anemia caused by the blood-sucking habits of the worms (Georgi and Georgi, 1990). At peak infection, naturally acquired populations of *H. contortus* may remove one-fifth of the circulating erythrocyte volume per day from lambs. Infections with as many as 500 worms, however, have been found to have little effect on the growth or wool production of sheep under conditions of satisfactory nutrition. In mountain reedbuck, the numbers of *H. contortus* needed for clinical signs of disease is unknown, but the mean of 116 worms per animal was probably negligible. The highest count was 1,050 worms in a young adult female, and this animal had a body condition similar to that of the rest of the animals culled at the same time.

Cooperia spp. usually play a secondary role in the pathogenesis of parasitic gastroenteritis of ruminants, but they may be the most numerous trichostrongyle present (Georgi and

Georgi, 1990). Although the number needed for clinical signs of disease is unknown, the average burden of 2,040 worms per animal would have been insignificant. The 15,000 worms found in 1 animal, however, might, in conjunction with other extenuating factors, result in some detrimental effects. This is speculative, because such effects have never been tested in wild antelope.

Possible causes of aggregation

Aggregation may be associated with heterogeneities in the host population, including host age, gender, body condition, behavior, and genetics (Wilson et al., 2002). It also may be associated with heterogeneities in the parasite population genetics or extrinsic factors, such as the spatial distribution of the parasites.

The most likely cause of heterogeneity in parasite loads (specifically, in *H. contortus*) was temporal variation in distributions of the parasite populations. Horak (1978a, 1978b, 1978c, 1978d, 1981) found that burdens of *H. contortus* in sheep, cattle, blesbok, and impala peaked between October and March at 4 sites in South Africa. Reinecke (1964, 1983) found that the abundance of *H. contortus* was positively correlated with ambient temperatures and rainfall. In summer rainfall areas, infective larvae on pasture increased after rains in excess of 15 ml per month and temperatures of greater than 17 C. Sheep acquired infection in November, and adult worms were dominant until February. At Sterkfontein, monthly rainfall only exceeded 15 ml after August, and at the time of the September 2000 and August 2001 culls, the rains had barely started. In addition, temperatures had not yet exceeded 17 C. Under this scenario, peak infections would have been expected only in the next culling periods (i.e., December 2000 and November 2001, respectively), and indeed, this was the case.

Host age could affect parasite distributions by a number of mechanisms, including parasite-induced host mortality and acquired immunity (Wilson et al., 2002). Although we found no evidence for a difference in parasite loads between animals of different ages, a thorough evaluation of age-associated heterogeneities was not possible in the present study because of the relatively small numbers of young and old animals sampled. Wilson et al. (2002) stated that sample sizes often decline with host age because of mortality, and if sampling effort is not directed at obtaining equal numbers of hosts in all age classes, then average parasite loads might appear to decline in old animals and parasite aggregation to decline with age, purely because of sampling biases.

Schalk and Forbes (1997) found that in 12 of 136 field studies on mammals, males exhibited a higher prevalence of parasites compared to females. In all 12 field studies, however, male biases were small (<5%). When meta-analyses were carried out using pooled data from these studies, including those that did not find male biases, males were still found to exhibit higher prevalences of parasites. Moore and Wilson (2002) found that the mean prevalence of infection was male-biased for helminths in mammals in general but not for Artiodactyla alone. Even if sex biases exist, determining the relative importance of the different mechanisms capable of generating them may prove to be extremely difficult, because many of the ecological and physiological factors covary (Wilson et al., 2002).

Intrinsic biological differences between host sexes could lead to 1 sex being more prone than the other to parasitic infections. Physiological, morphological, and behavioral differences between sexes could operate to create a slight but consistent sexual bias in infection levels. The present study, however, found no evidence of differences between males and females in parasite abundance.

Although no statistical differences were found between males and females in the present study, patterns of parasite loads were slightly different. Males had more worms than females between February and June, whereas females had more worms than males between August and December. One physiological aspect implicated in male-biased parasitism is that high testosterone levels can cause immunosuppression (Grossman, 1985). The main breeding season for mountain reedbuck was April/May, but if testosterone levels were higher at this time and males were immunosuppressed, then they should have had larger parasite loads. This, however, was not the case. The only nematode species that showed significant seasonal variation was *H. contortus*, and at Sterkfontein, males had their highest loads in December. Moreover, mountain reedbuck were considered to be nonseasonal (Irby, 1979), so significant peaks in testosterone secretion were unlikely to occur.

In females, evidence suggests that estrogens stimulate humoral and cell-mediated immunity (Schuurs and Verheul, 1990). In contrast, energetic costs of pregnancy and maternal care, plus the immunosuppressive effects of some hormones produced during parturition and lactation, may increase the susceptibility of females to parasites. Measuring immunocompetence is, however, fraught with difficulties (Wilson et al., 2002), because whether a simple relationship exists between immune function and disease susceptibility is unclear. Females at Sterkfontein had significantly more *H. contortus* in December than in May, June, August, and September, which is more consistent with the immunosuppression hypothesis during late pregnancy and parturition. Moreover, females that were lactating had significantly higher worm burdens than females that were still pregnant. Boomker (1990) found that the mean worm burden of lactating female kudu was more than double that of pregnant or quiescent females. The difference was ascribed to the stress associated with terminal pregnancy, parturition, lactation, and anxiety during the first few weeks of the newborn calf's life.

High parasite loads might decrease body condition, and this, in turn, will reduce resistance to parasitic infection. Body condition also is likely to affect the ability of hosts to compensate for damage inflicted by parasites, such as repairing tissues or replacing critical nutrients. At Sterkfontein, however, we found no correlation between numbers of parasites and body condition.

We are aware of few good examples of genetic variation in disease resistance in natural host populations, particularly in vertebrates. Even less research has been conducted on the importance of parasite heterogeneities. The effect of host or parasite genetics on parasitic infection rates was not within the scope of the present study.

Nematodes of TdR

No statistical tests were conducted on the parasite data from TdR; because prevalence and abundance of species were very low, any patterns would have had no biological meaning. Nematode burdens at TdR were much lower than at Sterkfontein. This lower abundance may have resulted from lower densities of mountain reedbuck at TdR. Arneberg et al. (1998) showed that for strongylid nematodes of mammals, abundance may depend on host-population density, because as host densities increase, each parasite egg or larva enjoys an increased probability of contacting a host. Differences in habitat also may have played a role. At TdR, grasses were clumped, and numerous bare patches of earth occurred between tufts. In contrast, at Sterkfontein, percentage grass canopy cover was very high, allowing infective larval nematodes greater opportunity to attach themselves to grass clumps to be eaten by grazers, such as mountain reedbuck.

Nematodes of gray rhebok at Sterkfontein

Four studies of gray rhebok at Bontebok National Park (Boomker et al., 1981; Horak et al., 1982; Boomker, 1990; Boomker and Horak, 1992) recorded 12 kinds of nematode, compared to 5 found at Sterkfontein. Those of the present study were, however, recovered from only 4 animals. Although the sample size was small, gray rhebok at Sterkfontein had fewer helminths compared to mountain reedbuck at the same site but had more helminths compared to mountain reedbuck at TdR. All the gray rhebok sampled were adults, but their ages were unknown. Two of the 4 were in poor condition.

Fecal egg counts and larval culture

Egg counts and larval counts were highly correlated, but neither was correlated with the number of adult worms within the intestinal tracts of the animals. This latter result is in agreement with previous findings that indicate the relationship between indirect measures and actual worm burden is very complex (Shaw and Dobson, 1995) and that egg counts are not a reliable method for estimating the numbers of parasites within the GIT (Reinecke, 1983). Gray rhebok larval counts were lower than those for mountain reedbuck at Sterkfontein, but because of the lack of correlation between larval counts and adult worm counts, little consequence can be attributed to this.

ACKNOWLEDGMENTS

Thanks to Mark and Tracey Roods, Cedric Barbé, Nacelle Collins, Hector Dott, Dominic Moss, Francois Nieuwoudt, Colin Oliver, Marie Smith, Francois van den Berg, and Savvas Vrahimis. Also to Free State Department of Tourism, Environment, and Economic Affairs for allowing the present study and to the following organizations that provided funding: the Faculty of Veterinary Science, University of Pretoria; the South African National Research Foundation; the Blundell Memorial scholarship; and the Maberly Memorial scholarship.

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Onderstepoort Journal of Veterinary Research, 73:311–314 (2006)

RESEARCH COMMUNICATION

Helminth parasites of gemsbok (*Oryx gazella*) in the Klein Karoo

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ABSTRACT

ELLIS, M.B. & BOOMKER, J. 2006. Helminth parasites of gemsbok (*Oryx gazella*) in the Klein Karoo. *Onderstepoort Journal of Veterinary Research*, 73:311–314

The number and species of helminth parasites from three gemsbok (*Oryx gazella*) were recorded, and their faecal nematode egg counts and the level of pasture contamination determined. Six nematode genera were recovered and four species identified, of which *Trichostrongylus rugatus* was the most prevalent. Other nematode species recovered were *Cooperia* sp., *Agriostomum* sp., *Haemonchus contortus, Nematodirus spathiger* and *Ostertagia ostertagi.* None of the worms were present in all animals studied, and no new host associations were found. Cysticerci were recovered from the mesenteries of one gemsbok and a further two unidentifiable helminths were recovered from the abomasum and the kidney fat layer of another antelope.

Keywords: *Agriostomum*, *Cooperia*, cysticerci, *Haemonchus*, *Nematodirus*, *Oryx gazella*, *Ostertagia*

INTRODUCTION

Gemsbok, *Oryx gazella*, are large antelope of the tribe Hippotragini, along with the seven surviving species of the genera *Oryx*, *Addax* and *Hippotragus*. Members of this tribe are typically large, stocky animals with long, ridged horns, and within the genus *Oryx* these horns are straight. The genus *Oryx* occurs throughout Africa in semi-desert and desert areas, but *O. gazella* is found mainly in southern Africa. Gemsbok are grazers, generally feeding on coarse semi-arid grass, supplementing their diet with roots and tubers (Kingdon 1997). In areas with higher rainfall gemsbok can form nomadic herds of up to 50 individuals, but in more arid areas tend to be solitary or in much smaller, looser social groups. Whilst solitary males have been seen to defend territories (Estes 1991), nomadic tendencies and the patchiness of food, such as "fertile islands", tends to restrict range establishment.

The helminths of these antelope have been listed by Round (1968). Boomker, Horak & De Vos (1986) added another five species and one genus of nematodes to the list and Boomker, Horak, Watermeyer & Booyse (2000) a further three nematode species.

This paper reports on the findings of an investigation of the parasites of gemsbok in Sanbona Wildlife Reserve in the Klein Karoo.

MATERIALS AND METHODS

Study site and animals

Sanbona Wildlife Reserve lies in the Western Cape Province approximately 200 km east of Cape Town (33°51' S; 20°33' E). The reserve is 54 000 ha in extent and is composed of Montagu Shale Rhenos-

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Accepted for publication 18 May 2006—Editor

terveld, transitional area North Langeberg Sandstone Fynbos and western Klein Karoo (R. Erasmus & K. Heunis, unpublished data 2004). The reserve is effectively split into two by the Warmwaterberg mountain range, resulting in a difference in the annual rainfall of 350 mm in the south and 200 mm in the north.

The first gemsbok were released onto the reserve in 1998 when it was still a Cape Wildlife Reserve. Sanbona, a private concern, acquired the reserve in 2002. A further 70 gemsbok were released in 2003 and the reserve currently holds 89 individuals. The antelope were captured in various localities throughout South Africa and it is possible that parasites not native to the Karoo have been introduced.

Three gemsbok were culled specifically for the helminth survey, and once thoroughly examined the carcasses were returned to the reserve to feed various carnivores in acclimatisation enclosures. Locations and details of culled animals are listed in Table 1. Mass and age were approximated by three workers and a consensus reached.

Pasture sampling

To check pasture larval contamination levels, ten plucks of foliage were taken every 10 m in a 10 m x 10 m grid to give a total of 100 sampling points and 1 000 plucks of vegetation. These were weighed and soaked overnight in warm water with 5 mℓ of detergent. Excess vegetation was then removed and the suspension allowed to sediment. The supernatant was gradually removed to leave a concentrated pellet of herbage and nematode larvae. These samples were re-suspended in a minimum of distilled water and larvae counted. Larval presence was recorded as the number of larvae per kg wet herbage.

Recovery of helminths

A full post-mortem examination was carried out on each individual, which involved the dissection of the heart, lungs, liver, and kidneys for determining the presence of helminths. A gross dissection of the masseter muscles was performed to locate metacestodes.

Carcasses that had to be transported for a long distance were opened and the organs ligated at appropriate locations to prevent mixing of gut contents or movement of parasites. The various parts of the intestinal tract were isolated as soon as possible after culling and opened down their length into separate containers with 5 ℓ physiological saline. The mucosa was stripped down its entire length between thumb and forefinger into the container and left to incubate at 37 °C with occasional stirring. After 3 h the mucosa was once again stripped into the container and the tissue discarded. The contents of the containers were made up to 5 ℓ with water, and two 250 mℓ sub-samples were taken and preserved with 10 mℓ formalin. The two sub-samples were combined and examined under a dissecting microscope for helminths. The helminths recovered were identified, coded and stored in formalin.

Faecal worm egg counts

Faeces were collected from the rectum of culled gemsbok to ensure correct identity of the specimen. A 4 g sample of faeces was added to 56 mℓ of saturated saline, thoroughly mixed with a glass rod and passed through a 100 µm sieve. The number of eggs per gram of faeces were then counted using a McMaster slide, and an average of three slides taken as the individual's faecal worm egg count.

Molecular bar-coding of unidentified samples

Bar-coding of the first 600 base pairs of the 18s (SSU) gene of nematodes was attempted as described by Blaxter, De Ley, Garey, Liu, Scheldeman, Vierstraete, Vanfleteren, Mackey, Dorris, Frisse, Vida & Thomas 1998; Dorris, De Ley & Blaxter 1999, and the first three divergent loops of the 28s (LSU) gene of the cysticerci (Littlewood, Curini-Galletti & Herniou 2000; Olson, Littlewood, Bray & Mariaux 2001). Cell digests were carried out according to the methods of Stanton, McNicol & Steele (1998), and PCR was performed as per the cited protocols.

RESULTS

Animal C had a much higher count and more diverse range of parasites than the other two study animals (Table 1). This included more than 20 cysticerci (2–10 cm) that were attached to the mesentery and two unidentifiable nematodes found in the abomasum and kidney fat layer. This was also the only individual that harboured *Cooperia* spp. in addition to the other identified nematode species. Unfortunately however it was not possible to identify the *Cooperia* spp. to species level.

Agriostomum sp. was the most numerous genus, but this is based on a single large infection in Animal C, biasing the count. *Trichostrongylus rugatus* was

TABLE 1 Collection data and helminths recovered from gemsbok in the Klein Karoo

Animal no.	**A**	**B**	**C**
Age Sex Mass (kg)	6 yr Female 170	6 yr Female 140	4 yr Female 120
Helminths			
Agriostomum sp. *Cooperia* sp. *Haemonchus contortus* *Nematodirus spathiger* *Ostertagia ostertagi* *Trichostrongylus rugatus*	50 0 10 30 0 90	0 0 0 0 0 30	> 1 000 50 70 120 90 80
Total no. of helminths	180	30	> 1 410
Faecal worm egg count	293	223	1508

the next most numerous and the most prevalent, and Animal B was infected with only this nematode.

At the site where Animal A was culled there were 1 550 larvae per kg wet herbage, where Animal B was culled there were 217 larvae and where Animal C was culled there were 1 444 larvae. Faecal worm egg counts were low in animals A and B (Table 1), which had low intensities of adult helminth despite the high larval counts on the herbage.

Attempts to identify the unknown nematodes from the abomasum and the body cavity using molecular techniques failed. This is most likely due to the effects on DNA of storage of these specimens in unbuffered formalin, leading to formalin-DNA-protein cross-linking which inhibits PCR amplification (Karlsen, Kalantari, Chitemerere, Johansson & Hagmar 1994; Schander & Halanych 2003).

DISCUSSION

A single gemsbok in the Kalahari Gemsbok National Park had a total of 5 877 nematodes (Boomker *et al.* 1986), two gemsbok from the Western Coast National Park (33°6'–33°10' S; 17°57'–18°2' E; Altitude 0–50 m) had an average of 28 391 worms (Boomker *et al.* 2000) and 24 antelope from the Free State had an average of 1 506 (Fourie, Vrahimis, Horak, Terblanche & Kok 1991). With the exception of Animal C, which was more heavily infected, the absolute number of parasites collected seem considerably lower in this study than in the two studies conducted by Boomker *et al.* (1986, 2000). It is possible that the overdispersion in Animal C is due to it having been captured at a site with high levels of *Agriostomum* and *Cooperia*, and on release at Sanbona was exposed to novel parasites leading to an increased infection rate.

The helminths of grey duiker in the same region were also investigated as part of this study. Their data are not included as only three cysticerci and one unidentified nematode were found in six individuals. The small numbers of parasites recovered are probably related to the nature of the Reserve and the drought that prevailed at the time.

Cooperia spp. are generally regarded as relatively harmless to well nourished and low stressed animals (Reinecke 1983), and the number recovered from Animal C is negligible. *Cooperia* spp. were not recovered from the gemsbok in the West Coast National Park. *Trichostrongylus rugatus* is primarily a parasite of the non-seasonal and summer rainfall areas (Reinecke 1983) but was the predominant nematode in gemsbok in the West Coast National Park, which is in the winter rainfall area (Boomker *et al.* 2000). Since the numbers of helminths recovered from the gemsbok in this study were small and that no signs disease or injury were noticed we conclude that the burdens were neglible.

Further studies using molecular techniques to identify helminths should be encouraged, but samples should be stored in ethanol or buffered formalin. However, there are problems associated with both options. Ethanol is an excellent preservative for DNA studies but can cause bloating and disruption of morphological characters, and buffered formalin, though better than unbuffered, still presents problems associated with DNA cross-linkage, which can reduce the effectiveness of amplification techniques.

ACKNOWLEDGEMENTS

We thank the staff of Sanbona Wildlife Reserve for making the antelope available to us and for their valuable assistance in the field, and Mr James Kitson for his assistance in processing the animals. This work was conducted with the financial assistance of the Weir Fund for Field Studies and the James Rennie Bequest.

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ARTHROPOD PARASITES

Onderstepoort J. vet. Res., 50, 221–228 (1983)

THE IXODID TICK BURDENS OF VARIOUS LARGE RUMINANT SPECIES IN SOUTH AFRICAN NATURE RESERVES

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ABSTRACT

HORAK, I. G., POTGIETER, F. T., WALKER, JANE B., DE VOS, V. & BOOMKER, J., 1983. The ixodid tick burdens of various large ruminant species in South African nature reserves. *Onderstepoort Journal of Veterinary Research*, 50, 221–228 (1983).

The ixodid tick burdens of eland (*Taurotragus oryx*), greater kudu (*Tragelaphus strepsiceros*), nyala (*Tragelaphus angasi*), bushbuck (*Tragelaphus scriptus*) and giraffe (*Giraffa camelopardalis*) in the Kruger National Park, Transvaal; of African buffalo (*Syncerus caffer*) and nyala in the Hluhluwe Game Reserve, Natal; and of gemsbok (*Oryx gazella*) in the Mountain Zebra National Park, an eland in the Thomas Baines Nature Reserve and an eland and greater kudu in the Andries Vosloo Kudu Reserve, eastern Cape Province, were determined.

The tick burdens of animals shot at the same time and locality are compared, and the attachment sites of some tick species on some of the hosts are given.

INTRODUCTION

During the past few years a number of surveys have been undertaken to determine the ixodid tick burdens of various wild ruminants in the Republic of South Africa. In this way the tick burdens of greater kudu (*Tragelaphus strepsiceros*); springbok (*Antidorcas marsupialis*); impala (*Aepyceros melampus*); blesbok (*Damaliscus dorcas phillipsi*); bontebok (*Damaliscus dorcas dorcas*), and vaal ribbok (*Pelea capreolus*) have been ascertained in different localities (Knight & Rechav, 1978; Horak, Meltzer & De Vos, 1982; Horak, 1982; Horak, Brown, Boomker, De Vos & Van Zyl, 1982; Horak, De Vos & De Klerk, 1982).

In this paper additional data are given on greater kudu, plus information on tick burdens of nyala (*Tragelaphus angasi*), bushbuck (*Tragelaphus scriptus*), eland (*Taurotragus oryx*), African buffalo (*Syncrus caffer*), giraffe (*Giraffa camelopardalis*) and gemsbok (*Oryx gazella*).

MATERIALS AND METHODS

The animals examined were either culled specifically for survey purposes or were shot or found dead because of injury or disease. The species of animals examined and the localities in which they were obtained are summarized in Table 1.

Ixodid ticks were recovered from these animals using the methods described by Horak *et al*. (1982). The skins of the nyala and buffalo from the Hluhluwe Game Reserve, however, were not immersed in a tick detaching agent but were transported in a weak solution of formalin in plastic bags to the laboratory at Onderstepoort. There they were scrubbed and washed in the same manner as the other skins.

Immature ticks and adult, unengorged *Boophilus decoloratus* were counted and identified by examining all the collected material, or representative samples of it, under a stereoscopic microscope. The representative samples were obtained by increasing the volume of the collected material to approximately 800 mℓ by the addition of water. The material was thoroughtly mixed by rapidly pouring it from one container to another and then pouring exactly ½ of it into 1 of the containers. This ½ could be further divided after making it up to approximately 800 mℓ and following the same procedure as mentioned above. The usual size of the samples examined varied between ½ and ⅛ of the total, and an attempt was made to count and identify at least 300 immature ticks from each animal. The smallest samples examined were $^{1}/_{64}$th of the material form the skins of the buffaloes' necks, bodies and upper legs.

TABLE 1 Species of animals examined and localities in which they were obtained

Animals examined	Province	Locality	Co-ordinates	Altitude (m)	Vegetation as classified by Acocks (1975)
Eland	Transvaal (Kruger National Park)	Near Pretoriuskop	25°10′S; 31°16′E	600	Lowveld Sour Bushveld
Giraffe		Near Lower Sabie	25°07′S; 31°55′E	180	Lowveld
Greater kudu, bushbuck		Skukuza	24°58′S; 31°36′E	262	Lowveld
Greater kudu, bushbuck, nyala		Near Pafuri	23°27′S; 31°19′E	305	Mixed Bushveld
African buffalo, nyala	Natal	Hluhluwe Game Reserve	28°07′S; 32°03′E	150–450	Zululand Thornveld and Lowveld
Gemsbok	Cape Province	Mountain Zebra National Park	32°15′S; 24°41′E	1 200–1 957	Karroid *Merxmeullera* Mountain Veld replaced by Karoo
Eland		Thomas Baines Nature Reserve	33°23′S; 26°28′E	335–518	False Macchia, Eastern Province Thornveld and Valley Bushveld
Eland, greater kudu		Andries Vosloo Kudu Reserve	33°07′S; 26°40′E	300–450	Valley Bushveld

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Received 6 June 1983—Editor

TABLE 2 The ixodid tick burdens of eland, kudu, nyala, bushbuck and giraffe in the Kruger National Park

Host	Sex	Age	Date culled (C) or died (D)	Numbers of ixodid ticks recovered																								
				Amblyomma hebraeum				*Boophilus decoloratus*				*Rhipicephalus appendiculatus/ zambeziensis*	*Rhipicephalus appendiculatus*			*Rhipicephalus zambeziensis*			*Rhipicephalus evertsi evertsi*				*Rhipicephalus pravus group*	*Rhipicephalus kochi*			*Rhipicephalus simus*	
				L	N	♂	♀	L	N	♂	♀	L	N	♂	♀	N	♂	♀	L	N	♂	♀	L	N	♂	♀	♂	♀
Pretoriuskop																												
Eland*	F	Old	27 Sept 1979 (D)	4 128	1 704	744	153	384	96	144	0	112	352	0	0	16	0	0	64	0	9	0	0	0	0	0	1	0
Eland	M	6 weeks	1 Oct 1979 (C)	328	16	27	6	104	264	80	68 (4)	16	8	0	0	0	0	0	24	80	1	0	0	0	0	0	3	0
Skukuza																												
Bushbuck**	F	Adult	9 Oct 1979 (D)	5	12	2	0	23	31	3	1	9	0	0	0	105	0	0	0	0	1	0	0	0	0	0	0	0
Bushbuck***	M	Yearling	5 Aug 1980 (D)	51	22	4	2	268	114	51	23 (1)	472	3	0	0	604	0	0	8	1	0	0	0	0	0	0	0	0
Bushbuck	M	2 years	31 Oct 1980 (D)	58	79	0	0	162	75	9	0	4	0	1	1	94	1	1	4	6	0	0	0	0	0	0	0	0
Bushbuck****	M	6 months	14 June 1982 (D)	726	4	0	0	698	554	104	50	748	16	0	0	0	0	0	32	48	0	0	0	0	0	0	0	0
Bushbuck	F	Adult	11 Nov 1982 (D)	17	41	10	7	4 977	1 847	680	366 (21)	8	0	0	6	258	2	0	16	0	0	0	0	0	0	0	0	0
Bushbuck	M	Adult	15 Nov 1982 (D)	168	16	10	2	1 436	1 184	720	254 (4)	0	16	0	2	50	2	2	0	0	0	0	0	0	0	0	0	0
Bushbuck*****	F	Adult	17 Nov 1982 (D)	1 798	158	2	0	3 862	86	28	10	24	54	0	0	34	0	0	128	0	4	2	0	0	0	0	0	0
Bushbuck	M	Adult	18 Nov 1982 (D)	256	80	0	0	1 658	636	216	48	0	0	2	0	40	2	2	4	0	0	0	0	0	0	0	0	0
Kudu	M	Sub-adult	31 July 1980 (C)	16	2	0	0	64	0	18	12 (3)	368	16	0	0	96	0	0	8	16	1	0	0	0	0	0	0	0
Kudu	M	Adult	31 July 1980 (C)	80	144	10	3	112	128	144	34 (1)	752	112	0	1	240	1	1	0	0	2	0	0	0	0	0	0	0
Lower Sabie																												
Giraffe†	M	Adult	24 July 1980 (C)	624	272	585	167	2 208	1 600	464	132 (4)	1 376	592	0	0	0	0	0	448	48	2	2	0	0	0	0	0	0
Giraffe††	M	Adult	25 July 1980 (C)	128	160	360	112	192	320	256	137 (8)	80	32	0	0	0	0	0	0	0	10	2	0	0	0	0	2	0
Pafuri																												
Kudu	M	15–18 months	5 Oct 1981 (C)	218	78	4	2	981	1 092	253	156 (8)	0	232	0	0	0	0	0	16	0	4	0	136	48	20	7	0	0
Kudu	M	Adult	5 Oct 1981 (C)	161	56	2	0	643	896	424	102 (6)	0	150	0	0	0	0	0	24	4	0	2	64	66	14	12	0	0
Nyala	M	Adult	6 Oct 1981 (C)	56	4	3	0	32	14	16	10 (2)	28	249	0	0	24	0	0	0	0	0	0	250	308	42	34	0	0
Nyala	M	Adult	7 Oct 1981 (C)	0	12	0	0	121	105	85	30 (6)	24	300	0	0	12	0	0	0	0	0	0	280	200	29	26	0	0
Bushbuck	M	Adult	6 Oct 1981 (C)	8	76	0	0	48	8	4	0	69	148	0	0	44	0	0	1	0	0	0	236	112	34	54	0	0
Bushbuck	M	Old	8 Oct 1981 (C)	48	17	5	3	12	28	4	2 (2)	20	285	0	0	0	0	0	0	0	0	0	56	32	25	20	0	0
Bushbuck	F	Adult	8 Oct 1981 (C)	4	84	0	2	13	12	8	0	16	17	0	0	39	0	0	0	0	0	0	448	217	37	17	0	0

* *Haemaphysalis aciculifer* 2 ♂♂, ***Ixodes* sp. 6 nymphae, ****Ixodes* sp. 1 larva, 2 nymphae, *****Ixodes* sp. 28 larvae, ******Ixodes* sp. 16 larvae, ( ) = No. of ♀♀ *B. decoloratus* between 4,0 and 7,0 mm in lenght, † *Hyalomma truncatum* 6 ♂♂, †† *H. truncatum* 4 ♂♂, 4 ♀♀, L = Larvae, N = Nymphae

Maturing *B.decoloratus* females and adult ticks of other species where separated out by macroscopically examining the material *in toto* after the representative sample had been examined, and the ticks were identified and counted under the stereoscopic microscope.

The immature stages of the *Ixodes* spp. recovered were not specifically identified. No attempt was made to differentiate the larval stages of *Rhipicephalus appendiculatus, Rhipicephalus maculatus, Rhipicephalus muehlensi* and *Rhipiciphalus zambeziensis* when 2 or more of these species were present on the same host.

RESULTS

Kruger National Park

A total of 10 ixodid tick species were recovered from the animals examined in this park (Table 2). The adult eland and the giraffe harboured large numbers of adult *Amblyomma hebraeum*. At Skukuza, in the south of the park, nymphae of *R. zambeziensis* were more numerous than those of *R. appendiculatus*. At Pafuri, in the north, the converse was true. Larvae of the *Rhipicephalus pravus* group and nymphae and adults of *Rhipicephalus kochi* constituted a large proportion of the total tick burdens on all the animals at Pafuri. These ticks, however, were absent on all the animals from the localities in the south of the park. The kudu at Pafuri harboured considerably more *A. hebraeum* and *B. decoloratus* than the nyala or bushbuck shot during the same week from the same locality. These in turn harboured more *R. zambeziensis* and *R. kochi* and generally more *R. pravus* group larvae than the kudu.

Not only did the numbers of *B. decoloratus* harboured by the 3 antelope species at Pafuri differ considerably, but there was also a difference in the proportional distribution of this tick on the various hosts (Table 3).

TABLE 3 The proportional distribution of *Boophilus decoloratus* on kudu, nyala and bushbuck at Pafuri

Host	Mean No. of *B. decoloratus* recovered	Percentage of *B. decoloratus* recovered from			
		Head	Neck, body and upper legs	Lower legs and feet	Tail
Kudu	2 274	29,0	34,4	36,1	0,5
Nyala	207	14,5	4,9	79,9	0,7
Bushbuck	46	37,4	5,8	53,2	3,6

Approximately equal proportions of the *B. decoloratus* burden were recovered from the heads; the necks, bodies and upper legs; and lower legs and feet of the kudu. On both the nyala and bushbuck more than 50% of the ticks were recovered from the lower legs and feet and very few from the necks, bodies and upper legs.

Hluhluwe Game Reserve

Nine species of ixodid ticks were recovered from the buffalo and nyala shot in this reserve (Table 4). The buffalo were excellent hosts of all stages of development of *A. hebraeum*, the larvae of *Rhipicephalus* spp., the nymphae of *R. appendiculatus*, the nymphae and adults of *R. maculatus* and the adults of *Rhipicephalus simus*. The nyala were excellent hosts of the nymphae and adults of *R. muehlensi*, good hosts of the larvae of *Rhipicephalus* spp., and fair hosts of the nymphae of *R. appendiculatus* and *R. maculatus*. The majority of adult *A. hebraeum* and adult *R. maculatus* were recovered from the less hairy undersides of the buffalo, from the axilla to the escutcheon, while the majority of *R. meuhlensi* were recovered from the heads of the nyala.

Mountain Zebra National Park

Seven ixodid tick species were recovered from the gemsbok shot in this park (Table 5). Of these *Margaropus winthemi* and *Rhipicephalus glabroscutatum* were the most numerous.

Thomas Baines and Andries Vosloo Reserves

Nine ixodid tick species were recovered from the eland from the Thomas Baines Reserve, and 8 and 7 species from the eland and kudu, respectively, from the Andries Vosloo Reserve (Table 6).

The eland from the Thomas Baines Reserve haboured large numbers of all stages of development of *A. hebraeum, Haemaphysalis silacea* and *Rhipicephalus evertsi evertsi* plus larvae and adults of *R. appendiculatus*. The eland from the Andries Vosloo Reserve was heavily infested with larvae and adults of *A. hebraeum* and moderately infested with adult *R. appendiculatus* and *R. glabroscutatum*. The kudu, which had either died or been shot because of injury or exhaustion while being translocated, were moderately to heavily infested with all stages of development of *H. silacea* and the immature stages of *A. hebraeum, R. appendiculatus, R. evertsi evertsi* and *R. glabroscutatum*.

The proportional distributions of some of the ticks infesting the kudu are summarized in Table 7.

The larvae and nymphae of *A. hebraeum, H. silacea* and *R. glabroscutatum* and the *R. appendiculatus* larvae showed a preference for the lower legs and feet. The nymphae and adults of *R. appendiculatus* and larvae and nymphae of *R. evertsi evertsi* preferred the heads of the kudu. The largest proportion of male *H. silacea* were found on the neck, body and upper legs of the kudu, while the number of females found on the tail exceeded the total number of females attached elsewhere.

DISCUSSION

Several ticks had probably detached and left the skins of the animals that had died as a result of injury or disease before the carcasses of these animals could be brought to the laboratories and processed for tick recovery. This fact must be borne in mind when considering the tick burdens of these animals; they might have been considerably larger had it been possible to collect them immediately after the host's death.

The large number of dead bushbuck that were examined at Skukuza can be ascribed to the fact that these animals come into the staff village at night during the winter and spring months. Here they browse on the green garden shrubs and, if alarmed, may jump into a garden fence and break their necks. Others, dazzled by the bright headlights, are killed by cars.

With the exception of those of the buffaloes and the single eland from the Thomas Baines Reserve, none of the tick burdens harboured by the animals were particularly large. It is perhaps interesting to speculate what the total tick burdens of the buffaloes and the eland might have been had *B. decoloratus* also been present in large numbers in the Hluhluwe and Thomas Baines Reserves. The eland had a broken tooth and was emaciated, conditions which possibly made the animal more susceptible to infestation and accounted for its large tick burden. The buffaloes, however, were apparently all healthy.

The really large burdens of most developmental stages of the majority of tick species carried by the buffaloes suggest that, in those regions where these animals still occur, they must be regarded as amongst the most important hosts of ixodid ticks. This observation supports that of Dinnik, Walker, Barnett & Brocklesby (1963), who

TABLE 4 The ixodid tick burdens of buffalo and nyala in the Hluhluwe Game Reserve

Host	Sex	Age	Date slaughtered	Numbers of ixodid ticks recovered																							
				Amblyomma hebraeum				*Boophilus decoloratus*		*Haemaphysalis silacea*			*Rhipicephalus* spp.	*Rhipicephalus appendiculatus*			*Rhipicephalus maculatus*			*Rhipicephalus muehlensi*			*Rhipicephalus evertsi evertsi*			*Rhipicephalus simus*	
				L	N	♂	♀	L	♀	N	♂	♀	L	N	♂	♀	N	♂	♀	N	♂	♀	N	♂	♀	♂	♀
Buffalo	M	Sub-adult	6 Sept 1978	339	203	270	83	0	0	0	0	2	5 896	5 509	20	1	3 106	40	9	81	4	2	0	8	1	18	6
Buffalo	F	Adult	6 Sept 1978	148	405	323	49	0	0	0	1	0	5 220	6 221	0	0	1 933	31	27	0	14	18	0	12	10	39	20
Buffalo	F	Adult	7 Sept 1978	712	407	1 092	248	64	0	0	0	0	5 792	5 275	6	3	4 073	268	68	64	0	0	0	9	1	9	4
Buffalo	F	Adult	7 Sept 1978	220	228	347	167	0	0	0	0	0	9 704	5 552	12	9	6 376	284	120	1	0	0	1	7	1	4	13
Nyala*	M	Sub-adult	8 Sept 1978	40	34	5	0	24	16	8	1	0	3 552	1 672	0	1	152	3	4	312	206	72	0	1	0	0	0
Nyala**	M	Sub-adult	8 Sept 1978	192	26	2	0	0	0	0	2	2	2 232	856	0	0	872	0	0	2 000	369	218	0	0	0	0	0

* = *Ixodes pilosus* 1 ♂, 5 ♀♀
** = *Ixodes* sp. 16 larvae; *Ixodes* sp. 1 ♀ (probably *I. pilosus* but damaged)
L = Larvae
N = Nymphae

TABLE 5 The ixodid tick burdens of 2 gemsbok shot in the Mountain Zebra National Park

Age	Numbers of ixodid ticks recovered																		
	Amblyomma marmoreum	*Hyalomma truncatum*		*Hyalomma marginatum turanicum*		*Margaropus winthemi*			*Rhipicephalus* sp.	*Rhipicephalus* sp. (near *R. capensis*)		*Rhipicephalus evertsi evertsi*				*Rhipicephalus glabroscutatum*		
	N	♂	♀	♂	♀	N	♂	♀	L	♂	♀	L	N	♂	♀	N	♂	♀
Young adult	2	1	2	14	3	22	88	81	4	9	7	8	0	27	15	2	103	51
Adult	0	3	1	18	14	20	56	34	8	3	9	0	3	38	10	4	111	40

L = Larvae
N = Nymphae

remarked that buffalo in Uganda were so heavily infested with ticks that it was not possible to make total collections of these parasites. In contrast, Carmichael (1976) recovered only small burdens of adult ticks from 100 buffalo in Botswana. These animals had been immobilized in a foot-and-mouth disease investigation during which all visible ticks were collected. Carmichael (1976) attributed the small number of ticks partly to the fact that the collections were made towards the end of the seasonal long, dry period, and partly to the overall climate, which is sufficiently harsh to prevent the buildup of large numbers.

The composition of the burden of some tick species was undoubtedly related to the season during which the animals were slaughtered or had died. The majority of animals in the Kruger National Park and all the animals in the Hluhluwe Game Reserve were slaughtered or died during the months July–October (winter–spring) and generally carried fairly large numbers of nymphae of *R. appendiculatus*. This is the season in Southern Africa when nymphae of this tick reach peak numbers and few adults are present (Baker & Ducasse, 1967; Short & Norval, 1981 a, b,; Horak, 1982). Similarly, the large numbers of larvae of *R. appendiculatus* recovered from the eland and kudu during April and June, respectively, in the eastern Cape Province reflect the fact that these animals were examined in autumn and early winter, seasons when larvae of this tick reach peak numbers (Baker & Ducasse, 1967; Short & Norval, 1981 a, b; Horak, 1982.)

The recovery of large numbers of adult *A. hebraeum* from the eland, giraffe and buffalo in the Transvaal during winter and spring does not appear to be in accord with the findings of Norval (1977) and Knight & Rechav (1978) in the eastern Cape Province, or of Londt, Horak & De Villiers (1979) and Horak (1982) in the northern Transvaal. These authors all found adult *A. hebraeum* reached peak numbers during the summer months. In Natal, Baker & Ducasse (1967) recorded peak adult activity on cattle between September and January, a finding which more closely approximates to the present ones. It would, however, be necessary to examine eland, giraffe and buffalo at regular intervals throughout the year in the Kruger and Hluhluwe Parks to determine when the actual peaks in adult numbers occur and the number of ticks present at such times.

The very large numbers of adult *A. hebraeum* recovered from the eland, buffalo and giraffe, in comparison with the numbers collected from the somewhat smaller hosts such as kudu, nyala and bushbuck, suggest that the larger the host the more favourable it is for adult ticks of this species. The findings of Knight & Rechav (1978) support this contention in that, in a 13-month survey of the ticks of kudu in the eastern Cape Province, the greatest mean number of adult *A. hebraeum* they recovered from these animals was only 19. In a similar survey in the northern Transvaal, Horak (1982) recovered a mean of 80 adult *A. hebraeum* from cattle examined during February 1977, but impala from the same locality never harboured more than 1 adult tick of this species.

The *B. decoloratus* infestations encountered on animals in the Kruger National Park were never very large and, in general, adult ticks accounted for only a minor proportion of nearly every burden. However, a fairly high proportion of the adult females were over 4,0 mm in length, which probably indicates that they would engorge and detach within the next 24 h. In Australia, Wharton & Utech (1970) found that once the females of *Boophilus microplus* (which are somewhat larger than those of *B. decoloratus*) had reached a length of 4,5 mm they would complete their engorgement and drop within 24 h.

R. kochi has previously been recorded once only in South Africa, from an impala, also at Pafuri (Gertrud Theiler, unpublished data, 1964, as *Rhipicephalus neavei*). The numbers encountered in the present survey indicate that it must be regarded one of the major species of the Pafuri region.

Both host preference and host habitat probably played a role in the composition of the tick burdens of the buffalo and nyala in the Hluhluwe Game Reserve. The buffaloes generally prefer the savanna for grazing, while the nyala are found in the denser bush. From the findings in this survey it would appear that adult *A. hebraeum, R. evertsi evertsi, R. appendiculatus, R. maculatus* and *R. simus* prefer buffalo as hosts and that *R. muehlensi* prefers nyala. Adults of *Ixodes pilosus* were also found on nyala.

The Mountain Zebra National Park has a mean annual rainfall of only 398 mm, and the ticks recovered from the gemsbok there are mostly species associated with semi-arid conditions. *M. winthemi* is a 1-host tick which reaches peak numbers during the winter (Howell, Walker & Nevill, 1978), and the infestation may have been declining with the approach of summer. This might explain the absence of larvae and the relatively small numbers of nymphae recovered.

The numbers of ticks and tick species recovered from the gemsbok exceeded those recovered from blesbok slaughtered in the Mountain Zebra Park at the same time

TABLE 6 The ixodid tick burdens of eland and kudu in the eastern Cape Province

Host	Sex	Age	Date culled (C) or died (D)	Numbers of ixodid ticks recovered																											
				Amblyomma hebraeum				*Boophilus decoloratus*				*Haemaphysalis silacea*				*Ixodes* spp.		*Ixodes pilosus*		*Rhipicephalus appendiculatus*				*Rhipicephalus evertsi evertsi*				*Rhipicephalus glabroscutatum*			
				L	N	♂	♀	L	N	♂	♀	L	N	♂	♀	L	N	♂	♀	L	N	♂	♀	L	N	♂	♀	L	N	♂	♀
Thomas Baines Reserve																															
Eland*	M	Adult	29 April 82 (C)	6 352	320	1 443	189	16	48	13	4	3 600	432	881	264	304	80	4	10	4 760	40	1 185	222	992	144	127	18	0	0	0	0
Andries Vosloo Kudu Reserve																															
Eland**	M	Adult	4 March 83 (C)	1 159	52	1 195	134	0	0	0	0	331	32	179	24	0	0	0	2	94	0	205	165	152	40	49	6	880	156	198	164
Kudu	F	Adult	16 June 82 (D)	64	0	0	0	0	0	0	0	2 607	293	219	13	252	16	0	12	1 027	88	26	12	48	40	2	0	40	24	1	4
Kudu	M	Sub-adult	17 June 82 (C)	586	16	0	0	0	0	0	0	5 542	930	361	64	73	16	0	4	2 610	177	8	0	128	50	0	0	976	584	1	0
Kudu	F	Adult	17 June 82 (D)	625	52	0	0	0	0	0	0	1 497	226	83	13	0	0	0	0	2 341	376	46	10	321	80	0	0	5 846	1 296	6	1
Kudu	F	Adult	18 June 82 (D)	650	35	0	0	0	0	0	0	3 806	532	264	51	98	0	0	0	1 340	100	18	6	48	72	0	0	1 248	468	4	3
Kudu	M	Sub-adult	18 June 82 (D)	128	3	0	0	0	44	0	0	407	499	42	15	0	0	0	0	321	33	0	0	13	28	2	0	877	1 346	9	2

L = Larvae N = Nymphae

* Ixodes sp. 3 ♀♀; *Rhipicephalus* sp. (near *R. capensis*) 12 ♂♂, 1 ♀ and *Rhipicephalus simus* 20 ♂♂, 4 ♀♀

** *Hyalomma marginatum rufipes* 31 ♂♂, 6 ♀♀; *R. simus* 1 ♂, 1 ♀

TABLE 7 The proportional distribution of several tick species on 5 kudu in the Andries Vosloo Kudu Reserve

Tick species	Stage of development	Total No. recovered	Percentage recovered from			
			Head	Neck, body and upper legs	Lower legs and feet	Tail
Amblyomma hebraeum	Larvae	2 053	11,7	19,1	69,0	0,2
	Nymphae	106	15,1	5,7	76,4	2,8
Haemaphysalis silacea	Larvae	13 859	9,6	8,8	81,1	0,5
	Nymphae	2 480	6,1	7,4	85,8	0,7
	Male	969	1,2	39,2	35,5	24,1
	Female	156	1,3	34,6	0,6	63,5
Rhipicephalus appendiculatus	Larvae	7 639	22,7	21,6	55,0	0,7
	Nymphae	774	54,8	24,8	18,6	1,8
	Male	98	98,0	2,0	0,0	0,0
	Female	28	85,7	14,3	0,0	0,0
Rhipicephalus evertsi evertsi	Larvae	558	93,9	2,9	2,9	0,3
	Nymphae	270	90,4	6,7	2,9	0,0
Rhipicephalus glabroscutatum	Larvae	8 987	4,1	11,8	82,2	1,9
	Nymphae	3 718	1,5	7,7	88,9	1,9

(Horak *et al*., 1982). The gemsbok appeared to be under some stress in this park, which may not be a natural habitat of these animals (Ansell, 1971), and were not thriving, factors which may have made them more susceptible to tick infestation, as has been found with cattle under stress infested with *B. microplus* (Utech, Seifert & Wharton, 1978).

During a 13-month long survey of ticks on kudu on farms adjoining the Andries Vosloo Kudu Reserve, Knight & Rechav (1978) shot 2 kudu during June 1976 and 2 during June 1977. These authors visually examined certain areas on these kudu and removed, counted and identified the ticks they found (Knight, personal communication, 1982). They recovered no immature or adult *R. glabroscutatum* or *R. evertsi evertsi* and few larvae of *A. hebraeum, H. silacea* and *R. appendiculatus* from these animals. It is possible that these ticks were not present, or were present only in small numbers, but it is more likely that the techniques they used were not as sensitive as those employed in the present survey. Their survey did indicate, however, that the larvae and nymphae of *H. silacea* and *R. appendiculatus* can reach peak numbers during June.

Because they had recovered no immature *R. glabroscutatum* from any of the kudu examined in their survey, Knight & Rechav (1978) stated: "This indicates that the immature stages feed on other hosts, possibly small mammals, as does *Rhipicephalus simus* Koch or, even on birds, as is the case with *Hyalomma marginatum rufipes* Koch." The present findings contradict this statement in that fairly large numbers of immature *R. glabroscutatum* were recovered from nearly every host that was infested with adults of this species.

Perhaps the most significant finding of the present investigation is that large numbers of ticks may be found on apparently healthy wild animals. These burdens will probably be even larger if the recovery techniques used in the present survey are further improved.

ACKNOWLEDGEMENTS

We wish to thank the National Parks Board for placing the animals in the Kruger National Park and the Mountain Zebra National Park at our disposal. The Natal Parks Board kindly made available the buffalo and nyala in the Hluhluwe Game Reserve, and the Cape Provincial Administration the eland and kudu in the Thomas Baines and Andries Vosloo Reserves.

The assistance of Messrs B. D. de Klerk, C. Cheney, M. M. Knight and E. J. Williams with processing the necropsies is gratefully acknowledged.

This research was funded by the University of Pretoria and the Council for Scientific and Industrial Research.

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Printed by and obtainable from the Goverment Printer, Private Bag X85, Pretoria, 0001

Onderstepoort J. vet. Res., 55, 19–22 (1988)

ARTHROPOD PARASITES OF COMMON REEDBUCK, *REDUNCA ARUNDINUM*, IN NATAL

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ABSTRACT

HORAK, I. G., KEEP, M. E., FLAMAND, J. R. B. & BOOMKER, J., 1988. Arthropod parasites of common reedbuck, *Redunca arundinum*, in Natal. *Onderstepoort Journal of Veterinary Research*, 55, 19–22 (1988)

Twenty-five common reedbuck, *Redunca arundinum*, from the Himeville region, 21 from the Eastern Shores Nature Reserve, 4 from the Charter's Creek Nature Reserve and 2 from the St Lucia Game Park, Natal were examined for arthropod parasites. The reedbuck from Himeville were infested with 4 ixodid tick species, those from the Eastern Shores with 7 species and those from Charter's Creek and St Lucia with 6 species. *Rhipicephalus evertsi evertsi* was the only tick common to the 4 localities.

The lice *Damalinia reduncae* and *Linognathus fahrenholzi* were present on the reedbuck from each locality.

In addition 3 red duiker, *Cephalophus natalensis*, and 2 bushbuck, *Tragelaphus scriptus*, from the Charter's Creek Nature Reserve plus 2 impala, *Aepyceros melampus*, from the St Lucia Game Park were examined for ixodid ticks. The red duiker were infested with 3 tick species and the bushbuck and impala with 4 each.

INTRODUCTION

Common reedbuck *(Redunca arundinum)* are medium-sized antelope, the adult males having a mass of about 80 kg and females 70 kg (Smithers, 1983). The southern subspecies *Redunca arundinum arundinum* occurs in southern Africa as far north as southern Angola and the Zambezi River (Howard, 1983), but because of their specialised habitat requirements their distribution within these limits is patchy and discontinuous. In South Africa they are found in the central parts of the Transvaal and are widespread in Natal below 2 100 m. They are also present in the Transkei and east of the Komgha District in the Cape Province (Smithers, 1983).

Reedbuck have 2 essential habitat requirements, namely cover in the form of long grass, reedbeds or rocks, and a water supply. They avoid woodland but will tolerate the occurrence of woody vegetation within their grassland habitat. They live in pairs or family parties and are territorial. They do not form herds. When food and water are readily available reedbuck are nocturnal, but they may become more active during daytime in winter. They are almost exclusively grazers although they may browse in winter when the nutritive value of the grasses is low. Thus they respond to favourable agricultural practices where pastures are artificially irrigated during the winter months. They can take advantage of this high quality grazing all the year round, which may result in abnormally high populations being present. They are not strictly seasonal breeders: a single young may be born at any time of the year, after a gestation period of about 7,5 months.

Howard (1983) required culled reedbuck for his extensive 3 year study of the species and the opportunity was taken during the latter part of this project to collect material for parasite investigation. Permission was also obtained to remove 27 reedbuck from the eastern and western shores of Lake St Lucia to investigate their parasites. The arthropod parasites recovered from these animals are discussed in this paper.

The ixodid ticks of common reedbuck from countries in Africa outside the Republic of South Africa are recorded by Theiler (1962) and Walker (1974), while those occurring in South Africa are listed by Theiler (1962) and Baker & Keep (1970). The lice infesting these animals are listed by Ledger (1980).

MATERIALS AND METHODS

Study sites

Himeville

The animals examined were taken from 5 adjacent farms near Himeville (29° 43′ S; 29° 36′ E) in Natal. The area is situated between 1 550 and 2 000 m above sea level. The total rainfall for the 13 months during which the reedbuck were collected was 1 220 mm, most of which fell between October and March. The study site lies within the Highland Sourveld bioclimatic groups (Phillips, 1973). According to Acocks (1975) it supports forest and scrub forest, but very little of this now remains. The dominant vegetation type today is *Themeda-Apochaete* grassland; artificial, often irrigated, annual permanent pastures, and croplands of maize and Japanese radish. Natural woody plants are principally *Leucosidea* scrub along the waterways and a few patches of *Protea* savanna on hill slopes. Exotic species are mainly gums (*Eucalyptus* spp.), wattle *(Acacia* spp.) and pines *(Pinus* spp.).

In addition to common reedbuck other antelope species occurring in the area are eland, *Taurotragus oryx;* mountain reedbuck, *Redunca fulvorufula;* grey rhebok, *Pelea capreolus;* oribi, *Ourebia ourebi;* blesbok, *Damaliscus dorcas phillipsi,* and common duiker, *Sylvicapra grimmia*. As the area is primarily utilized for farming, cattle, sheep, and to a lesser extent horses, are the principal large mammals, nearly all of which are regularly dipped in acaricidal compounds, at least in the summer months.

St Lucia

Most of the animals (21) from this area came from the Eastern Shores Nature Reserve. For comparative purposes 2 were taken from the St Lucia Game Park and 4 from the Charter's Creek Nature Reserve of Lake St Lucia.

The Eastern Shores Reserve occupies an area of approximately 250 km^2 at the southern end of the Mozambique coastal plain, between 27° 51′ and 28° 25′ S latitude and 32° 20′ and 32° 40′ E longitude. The habitat favoured by reedbuck consists of low-lying, seasonally inundated grassland, within the Zululand Palm Veld subdivision of Coastal Thornveld and Coastal communities (Acocks, 1975).

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Received 2 October 1987—Editor

TABLE 1 Arthropod parasites recovered from 25 reedbuck from the Himeville region of Natal

Arthropod species	Total numbers of arthropods recovered					Number of animals infested
Ixodid ticks	Larvae	Nymphae	Males	Females	Total	
Boophilus sp.	38	0	0	0	38	9
Ixodes sp.	110	8	0	2	120	9
Rhipicephalus evertsi evertsi	760	504	0	1	1 265	22
Rhipicephalus sp.	2	0	12	13	27	4
Total	910	512	12	16	1 450	
Lice	Nymphae		Adults		Total	
Damalinia reduncae	1 765		2 321		4 086	22
Linognathus fahrenholzi	136		320		456	14
Total	1 901		2 641		4 542	

TABLE 2 Arthropod parasites recovered from 21 reedbuck from the Eastern Shores Nature Reserve in Natal

Arthropod species	Total numbers of arthropods recovered					Number of animals infested
Ixodid ticks	Larvae	Nymphae	Males	Females	Total	
Amblyomma hebraeum	14	2	0	0	16	5
Amblyomma marmoreum	12	0	0	0	12	2
Boophilus decoloratus	250	4	4	0	258	10
Haempahysalis sp.	2	6	0	0	8	2
Rhipicephalus spp.	28	—	—	—	28	9
Rhipicephalus appendiculatus	—	6	4	0	10	5
Rhipicephalus muehlensi	—	6	2	0	8	4
Rhipicephalus evertsi evertsi	1 162	808	0	6	1 976	19
Total	1 468	832	10	6	2 316	
Lice	Nymphae		Adults		Total	
Damalinia reduncae	84		144		228	7
Linognathus fahrenholzi	16		10		26	4
Total	100		154		254	

TABLE 3 Arthropod parasites recovered from 6 reedbuck from the Charter's Creek Nature Reserve and the St Lucia Game Park

Arthropod species	Total numbers of arthropods recovered					Number of animals infested
Ixodid ticks	Larvae	Nymphae	Males	Females	Total	
Amblyomma hebraeum	34	0	0	0	34	1
Haemaphysalis sp.	46	6	0	0	52	2
Rhipicephalus spp.	7 400	—	—	—	7 400	6
Rhipicephalus appendiculatus	—	748	130	132	1 010	6
Rhipicephalus maculatus	—	252	0	0	252	4
Rhipicephalus muehlensi	—	84	2	0	86	3
Rhipicephalus evertsi evertsi	160	150	0	2	312	6
Total	7 640	1 240	132	134	9 146	
Lice	Nymphae		Adults		Total	
Damalinia reduncae	2		42		44	3
Linognathus fahrenholzi	32		8		40	1
Total	34		50		84	

The hottest month is February and the coolest July, and the total average rainfall is 1 109 mm. The wettest months are January to April and the driest July to September.

The population density of reedbuck on the Eastern Shores of Lake St Lucia (0,46 per ha) appears to be amongst the highest in Africa (Venter, 1979). Besides reedbuck, other major mammal species occurring in the Eastern Shores Reserve include hippopotamus *(Hippopotamus amphibius)*, numbering approximately 600; bushpig *(Potamochoerus porcus)*, and buffalo *(Syncerus caffer)*, numbering about 40 at the time of this study.

The St Lucia Game Park is an enclosed area at the southern end of the Eastern Shores Reserve containing, besides reedbuck, waterbuck *(Kobus ellipsiprymnus)*; blue wildebeest *(Connochaetes taurinus)*; impala *(Aepyceros melampus)*, and warthog *(Phacochoerus aethiopicus)*.

The Charter's Creek Nature Reserve lies immediately west of the Eastern Shores Reserve and consists of similar habitat to this reserve. Other mammals present there include bushbuck *(Tragelaphus scriptus)*; nyala *(Tragelaphus angasii)*; common duiker and steenbok *(Raphicerus campestris)*. The reedbuck density there is much higher (0,86 per ha) than in the Eastern Shores Reserve.

Survey animals

At Himeville 2 reedbuck (1 adult and 1 subadult) were shot each month for 13 consecutive months from May 1983–May 1984. Two to 4 reedbuck were shot at 3–4 monthly intervals in the Eastern Shores Nature Reserve from March 1983–August 1984. Two reedbuck were shot in the St Lucia Game Park during May 1984 and 4 in the Charter's Creek region during August 1984.

In addition to the reedbuck, 3 red duiker, *Cephalophus natalensis*, and 2 bushbuck in the Charter's Creek region, and 2 impala in the St Lucia Game Park, were shot and examined for parasites.

Parasite recovery

Only 1 half of each animal was processed for arthropod recovery, otherwise the animals were treated as described by Horak, Meltzer & De Vos (1982). The tick burdens of these animals were determined as described by Horak, Potgieter, Walker, De Vos & Boomker (1983).

RESULTS

The parasite burdens of the 3 groups of reedbuck and of the red duiker, bushbuck and impala are summarized in Tables 1–4.

Twenty-five of the 26 reedbuck from Himeville were examined for ectoparasites. These animals harboured 4 ixodid tick species, of which *Rhipicephalus evertsi evertsi* was the most abundant and prevalent. With the exception of the 25 adult *Rhipicephalus* sp. from the lower legs and feet of the 2 animals examined during July 1983, only 3 adult ticks were recovered. The total tick burdens of the animals were also very low and no pattern of seasonal abundance could be determined.

Seven ixodid tick species were recovered from the reedbuck examined in the Eastern Shores Nature Reserve. *R. evertsi evertsi* was again the most abundant and most prevalent tick. Only 16 adult ticks were recovered and the total tick burdens of the reedbuck were low.

The reedbuck from the St Lucia Game Park and the Charter's Creek Nature Reserve were infested with 6 tick species. The total tick burdens of these animals were higher than those of the reedbuck from the other localities and they also harboured more adult ticks.

The lice *Damalinia reduncae* and *Linognathus fahrenholzi* were recovered from reedbuck examined at each of the study sites.

The red duiker were infested with 3 tick species, and the bushbuck and impala with 4 each.

DISCUSSION

In addition to the ticks we recovered from the reedbuck Baker & Keep (1970) list *Ixodes pilosus*, *Haemaphysalis aciculifer*, *Haemaphysalis silacea*, *Rhipicephalus pravus* and *Rhipicephalus simus* as being found on animals in Natal.

One of the reasons for determining the parasite burdens of the reedbuck in the Himeville district was to ascertain whether they served as a reservoir of ticks that could infest the domestic livestock utilizing the same pastures. The fact that fewer than 1 500 ticks in total

TABLE 4 The tick burdens of red duiker, bushbuck and impala from the north-eastern regions of Natal

Date slaughtered	Numbers of ticks recovered																				
	Amblyomma hebraeum	*Boophilus decoloratus*				*Haemaphysalis* spp.	*Haemaphysalis parmata*			*Haemaphysalis silacea*			*Rhipicephalus* spp.	*Rhipicephalus appendiculatus*			*Rhipicephalus muehlensi*			*Rhipicephalus evertsi evertsi*	
	L	L	N	M	F	L	N	M	F	N	M	F	L	N	M	F	N	M	F	L	N
Red duiker, Charter's Creek Nature Reserve																					
March 1983	16					104	48	64	8				256				64				
March 1983	8					8	40	8					272				88				
July 1984*							10	20	6				32				60	2			
Bushbuck, Charter's Creek Nature Reserve																					
March 1983						24	72	40	26	8	2	2	384				176	99	74		
March 1983	56					120	32				6		1 760				368	114	76		
Impala, St Lucia Game Park																					
May 1984		16	4	12	20								1 900	28	80	112	4	2		116	92
May 1984**		36	30	18	16								1 664	16	4	6		2		48	28

* *Amblyomma marmoreum* Larvae 2; *Rhipicephalus maculatus* Nymphae 8

** With the exception of this animal, which was a juvenile male, all the other antelope were adult males

L = Larvae
N = Nymphae

M = Males
F = Females

were recovered from the 25 reedbuck examined indicates that in this particular habitat they pose no threat to domestic animals.

The animals from the Eastern Shores Nature Reserve, although infested with a greater variety of tick species than those from Himeville, also harboured only small numbers of ticks of which very few were adult. This led us to believe that the reedbuck could be a tick resistant antelope species similar to the blue and black wildebeest (Horak, De Vos & Brown, 1983). It is, however, possible that the Himeville and Eastern Shores localities are situated in regions of low tick infestation and consequently the reedbuck from the St Lucia Game Park and Charter's Creek Nature Reserve, which we assumed to have higher tick populations, were examined. These animals harboured considerably larger numbers of ticks than the other reedbuck, which indicates that where reedbuck are found in regions of high tick abundance they are likely to carry fairly large numbers of these parasites. Although the reedbuck and impala were examined during the same month in the St Lucia Game Park, the reedbuck harboured no *B. decoloratus* while both the impala were infested. In respect of other species the tick burdens of these animals were similar.

The red duiker were shot at Charter's Creek during March 1983 and July 1984 and the bushbuck during March 1983. All these animals were infested with *Haemaphysalis parmata,* while the reedbuck shot at this locality during August 1984 were not infested. This difference could be due either to seasonal differences in the abundance of the ticks, or differences in host preference, or differences in the habitat preferences of the antelope. Theiler (1962) comments on this tick as follows, "A Central and West African tick of the Guinean region that ranges into the forested highlands of Eastern Africa". The only record for South Africa she gives is Durban, Natal where she felt it may have been a recent introduction. The recovery of *H. parmata* from the animals at Charter's Creek indicates either that it has spread there from the Durban region or that originally it was more wide-spread than Theiler (1962) thought. The bushbuck seems to be a favoured host of this tick because Theiler's (1945) description of this species is based on material collected from a bushbuck in Uganda.

ACKNOWLEDGEMENTS

We wish to thank the Natal Parks Board for placing the antelope at our disposal.

We are grateful to Mrs Valerie A. Horak for her able technical assistance and Dr Jane B. Walker who confirmed the identification of *H. parmata*. This research was funded by the Meat Board, the Council for Scientific and Industrial Research and Rhodes University.

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Printed by the Government Printer, Private Bag X85, Pretoria, 0001

Onderstepoort J. vet. Res., 56, 63–66 (1989)

PARASITES OF DOMESTIC AND WILD ANIMALS IN SOUTH AFRICA. XXIV. ARTHROPOD PARASITES OF BUSHBUCK AND COMMON DUIKER IN THE WEZA STATE FOREST, NATAL

I. G. HORAK⁽¹⁾, M. E. KEEP⁽²⁾, A. M. SPICKETT⁽³⁾ and J. BOOMKER⁽⁴⁾

ABSTRACT

HORAK, I. G., KEEP, M. E., SPICKETT, A. M. & BOOMKER, J., 1989. Parasites of domestic and wild animals in South Africa. XXIV. Arthropod parasites of bushbuck and common duiker in the Weza State Forest, Natal. *Onderstepoort Journal of Veterinary Research*, 56, 63–66 (1989)

One bushbuck, *Tragelaphus scriptus*, and 1 common duiker, *Sylvicapra grimmia*, were shot each month from May 1983 to May 1984 in the Weza State Forest, Natal, i.e. a total of 13 animals of each species. The bushbuck were infested with 8 ixodid tick species, 2 louse species and a louse-fly species. The common duiker harboured 7 tick species and 2 louse species.

Ticks of the genus *Ixodes* were the most numerous and prevalent on both antelope species, but no pattern of seasonal abundance was evident. Although only small numbers were recovered, adult *Haemaphysalis aciculifer* were present from September to February, nymphs of *Rhipicephalus appendiculatus* from May to September, and adult *Rhipicephalus lunulatus* from December to March. The louse-fly, *Lipoptena paradoxa*, was recovered from some of the bushbuck from October to May.

INTRODUCTION

The distribution, habitats, habits and food preferences of bushbuck, *Tragelaphus scriptus*, and of common duiker, *Sylvicapra grimmia*, have been summarized and commented upon by Boomker, Keep & Horak (1987) and Boomker, Du Plessis & Boomker (1983) respectively.

The ixodid ticks of these animals in countries outside the Republic of South Africa have been recorded by Theiler (1962), Yeoman & Walker (1967) and Walker (1974). Those occurring in South Africa are listed by Theiler (1962) and Baker & Keep (1970), while Horak, Potgieter, Walker, De Vos & Boomker (1983) and Boomker *et al.* (1983) have determined the actual tick burdens of both species in the Transvaal.

The lice recovered from bushbuck and common duiker have been listed by Ledger (1980) and the flies by Haeselbarth, Segerman & Zumpt (1966). The louse and louse-fly burdens of common duiker have been determined by Boomker *et al.* (1983).

Allen-Rowlandson (1986) required freshly-killed bushbuck and common duiker for his study of these species within the Weza forestry areas of Natal. During the later part of his project, material for parasitological investigation was collected and the present paper records the arthropod parasite burdens of 13 animals of each species. The helminth burdens of these animals have been reported in a separate paper (Boomker *et al.*, 1987).

MATERIALS AND METHODS

Study site

The physiography of the Weza State Forest (30° 35′ S; 24° 45′ E), Alfred District of Natal, in which the animals were collected, has been described by Boomker *et al.* (1987).

Survey animals

One bushbuck and 1 common duiker were shot at night each month for 13 consecutive months from May 1983 to May 1984. Eleven adults and 2 sub-adults of each species were shot. These comprised 7 male and 6 female bushbuck and 8 male and 5 female duiker.

Parasite recovery

Immediately after slaughter the skins of the animals were processed for arthropod parasite recovery as described by Horak, Meltzer & De Vos (1982). The ectoparasite burdens of the animals were determined as described by Horak *et al.* (1983).

RESULTS

Bushbuck

The total numbers of arthropod parasites recovered from the 13 animals examined are summarized in Table 1.

The bushbuck were infested with 8 ixodid tick species, 2 louse species and a louse-fly species. Small numbers of adult *Haemaphysalis aciculifer* were recovered from each animal examined from September 1983 to February 1984. Ticks of the genus *Ixodes* were the most numerous and all animals were infested, but no pattern of seasonal abundance was evident. Three of the 5 antelope examined between December 1983 and April 1984 each harboured 2 adult *Rhipicephalus follis*, while the 3 animals examined between December and February were each infested with adult *Rhipicephalus lunulatus*. Six of the 8 antelope examined between October 1983 and May 1984 harboured the louse-fly *Lipoptena paradoxa*

Common Duiker

Table 2 summarizes the total numbers of arthropod parasites recovered from the 13 antelope examined.

The duiker harboured 7 ixodid tick species and 2 species of lice. The 3 animals examined between November 1983 and January 1984 were each infested with adult *H. aciculifer*. Although ticks of the genus *Ixodes* were the most numerous no pattern of seasonal abundance was evident. Each of the animals examined from May to September 1983 was infested with 2–4 nymphs of *Rhipicephalus appendiculatus*. Only the animal shot during March 1984 was infested with adult *R. lunulatus*.

DISCUSSION

Ixodid ticks

The bushbuck harboured more ticks of each species than did the duikers. In total they carried approximately 8 times more larvae, twice as many nymphs and 10 times

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Received 5 December 1988—Editor

TABLE 1 Arthropod parasites recovered from 13 bushbuck from the Weza State Forest, Natal

Arthropod species	Total numbers of arthropods recovered					Number of animals infested
Ixodid ticks	Larvae	Nymphs	♂♂	♀♀	Total	
Boophilus decoloratus	70	0	2	0	72	4
Haemaphysalis aciculifer	0	0	58	16	74	6
Ixodes spp.	42 502	4 568	—	—	47 070	13
Ixodes pilosus	—	—	212	978	1 190	13
Ixodes sp. (near *I. pilosus*)	—	—	64	930	994	12
Rhipicephalus appendiculatus	26	4	0	0	30	2
Rhipicephalus evertsi evertsi	788	120	0	0	908	9
Rhipicephalus follis	0	0	4	2	6	3
Rhipicephalus lunulatus	0	0	18	14	32	3
Total	43 386	4 692	358	1 940	50 376	
Lice	Nymphs		Adults		Total	
Damalinia natalensis	150		112		262	6
Linognathus panamensis	216		142		358	10
Total	382		258		640	
Flies	Adults				Total	
Lipoptena paradoxa	156				156	6

TABLE 2 Arthropod parasites recovered from 13 common duiker from the Weza State Forest, Natal

Arthropod species	Total numbers of arthropods recovered					Number of animals infested
Ixodid ticks	Larvae	Nymphs	♂♂	♀♀	Total	
Boophilus sp.	12	2	0	0	14	4
Haemaphysalis aciculifer	0	2	6	4	12	4
Ixodes spp.	5 370	2 140	—	—	7 510	13
Ixodes pilosus	—	—	21	124	145	12
Ixodes sp. (near *I. pilosus*)	—	—	15	58	73	10
Rhipicephalus appendiculatus	6	14	0	0	20	6
Rhipicephalus evertsi evertsi	92	20	0	0	112	9
Rhipicephalus lunulatus	0	0	2	0	2	1
Total	5 480	2 178	44	186	7 888	
Lice	Nymphs		Adults		Total	
Damalinia sp.	22		26		48	2
Linognathus breviceps-complex	30		50		80	8
Total	52		76		128	

more adults. MacLeod, Colbo, Madbouly & Mwanaumo (1977) have stated that the larger the host the more adult ticks it seems likely to carry. This is confirmed by the observations of Horak & Knight (1986) and Horak, Sheppey, Knight & Beuthin (1986). They determined the total tick burdens of various sympatric host species and found that, with some exceptions, the larger the animal species the better host it is, particularly for the adults.

Boophilus decoloratus

Horak *et al.* (1983) found that in habitats in which *B. decoloratus* abounds, such as the Kruger National Park, bushbuck are good hosts of this tick. The small number of ticks recovered from these animals in the present survey therefore probably indicates an unfavourable habitat. *B. decoloratus* prefers open grassland or savanna with an annual rainfall above 380 mm (Howell, Walker & Nevill, 1978), whereas the study area comprises mountain grassland (27 %), indigenous forest (19 %) and plantations of exotic trees (54 %) (Boomker *et al.*, 1987). The bushbuck and duiker examined in this study were shot in forested regions with variable grass cover depending upon the size of the trees. However, as only small numbers of *B. decoloratus* have been recovered from common duiker examined in a habitat suitable for the blue tick (Boomker *et al.*, 1983), duiker are in any event probably not good hosts for this species.

Haemaphysalis aciculifer

Hoogstraal & El Kammah (1972) have recorded bushbuck as a host of this tick in Uganda, Kenya and Tanzania and common duiker in Kenya. Walker (1974) also lists bushbuck and common duiker as hosts in Kenya. Its recovery from these animals in the Weza State Forest confirms the observation of Horak *et al.* (1986) that it has a wider distribution in South Africa than is given by Theiler (1962). Norval (1985) notes that the 7 collections made in Zimbabwe were all from animals in woodland or wooded grassland habitats on the high rainfall, highveld plateau. These collections, which consisted only of adults, were all made from November to January. In the south-western Cape Province Horak *et al.* (1986) recovered small numbers of adult ticks from grey rhebuck (*Pelea capreolus*) and bontebok (*Damaliscus dorcas dorcas*) from August to February. In the present survey adults were recovered from September to February.

Ixodes pilosus

We have assumed that the immature stages of this tick and those of the other *Ixodes* species recovered are indistinguishable, hence they are lumped under *Ixodes* spp. in the tables. *I. pilosus* is found in sourveld areas along the coast from Port Shepstone in Natal to Cape Town in the western Cape Province (Howell *et al.*, 1978). A total of 29 males and 102 females (a ratio of

1:3,5) were recovered by Norval (1974) from bushbuck and duiker in the eastern Cape Province. Horak, Jacot Guillarmod, Moolman & De Vos (1987) recovered 38 males and 130 females (a ratio of 1:3,4) from dogs and only 1 male and 39 females from caracals (*Felis caracal*) in the same region, while Horak *et al.* (1986) recovered 63 males and 205 females (a ratio of 1:3,3) from bontebok, grey rhebuck and scrub hares (*Lepus saxatilis*) in the south-western Cape Province. The animals from the Weza forest harboured a total of 233 males and 1 102 females (a ratio of 1:4,7). Norval (1974) suggests that these ratios indicate that mating may occur either on the host or on the ground.

Although no pattern of seasonal abundance was obvious in the present survey, Horak *et al.* (1986, 1987) found that in the south-western and eastern Cape Province the larvae peak in June and the nymphs in August, while the adults may peak from October to December or January to May. They suggested that only one life cycle was completed annually.

Ixodes sp.

These ticks resemble *I. pilosus*, but show definite palpal, coxal and setal differences and they probably represent a new species. One of us (A.M.S.) examined the *Ixodes* sp. collected from 2 blue duikers (*Cephalophus monticola*) during the National Tick Survey in Zimbabwe (Norval, Spickett & Clifford, 1987) and considers them to be identical to those collected in the present survey. No pattern of seasonal abundance is evident and the ratio of males to females is 1:12,5.

Rhipicephalus appendiculatus

Horak *et al.* (1983) and Boomker *et al.* (1983) recovered fair numbers of larvae and nymphs, but few adults, from bushbuck and common duiker examined in the Transvaal. None of those bushbuck were examined during late summer, the season of peak adult abundance, while some of the duiker were. The infestation at Weza was possibly maintained by cattle and goats which occasionally stray into the forest from surrounding farms (Boomker *et al.*, 1987). The period during which the nymphs were present (May–September) was slightly shorter than that of the peak nymphal abundance (April–October) observed by Knight & Rechav (1978) and Rechav (1982) on kudu (*Tragelaphus strepsiceros*), goats and cattle in the eastern Cape Province.

Rhipicephalus evertsi evertsi

Although no adult ticks were recovered this species was probably maintained by the mules and horses used as transport animals in the forest (Boomker *et al.*, 1987). Equids are the preferred hosts of this tick (Hoogstraal, 1956; Norval, 1981).

Rhipicephalus follis

The description of the male of *R. follis* by Theiler (1947) and the original illustrations by Dönitz (1910) were used to identify this species. The descriptions given under this name by Theiler & Robinson (1953) and the accompanying illustrations by D. Pringle are now thought to refer to another species. Theiler (1947) suggests that domestic stock are hosts of this tick. Although only very small numbers of adult ticks were recovered from the bushbuck these were present from December to April.

Rhipicephalus lunulatus

There has been considerable confusion in the past between this species and *Rhipicephalus tricuspis* (Walker, Keirans, Pegram & Clifford, 1988), but these authors have recently published redescriptions of both species, listed their host associations and illustrated their geographic distributions.

Norval & Tebele (1983) state that *R. lunulatus* is widely distributed in Zimbabwe in woodland or woodland/savanna habitats which receive 550–1 200 mm of rain per annum. Amongst the collections of adult ticks in that country, the majority of which were made from November to January, there is one from a common duiker. Colborne (1985) recovered adults from cattle in Zimbabwe from November to May. The preferred sites of attachment were the legs and tail. In the present study adult ticks were present from December to March and all but 2 were recovered from the lower legs of the bushbuck or duiker.

Lice

Both *Damalinia natalensis* and *Linognathus panamensis* are specific parasites of bushbuck (Ledger, 1980). The *Damalinia* sp. on the duiker could not be specifically identified, while the *Linognathus* sp. on this host belonged to the *Linognathus breviceps*-complex as discussed by Ferris (1932). Boomker *et al.* (1983) have recovered small numbers of *Damalinia lerouxi*, *L. breviceps* and *Linognathus zumpti zumpti* from common duikers in the central Transvaal. The lice burdens were never large on either of the antelope species and no patterns of seasonal abundance could be ascertained.

Flies

The louse-fly, *L. paradoxa*, has a wide host range among the antelope and many species that browse are infested (Haeselbarth *et al.*, 1966). Although some of the bushbuck in the present survey were infested none of the duikers were. This contrasts with the findings of Boomker *et al.* (1983), who recovered *L. paradoxa* from 12 of the 16 duikers they examined. In the present survey the flies were only recovered from October to May and then not from all the bushbuck examined during this period.

ACKNOWLEDGEMENTS

We wish to thank the Directorate of Forestry, Department of Environmental Affairs, for placing the animals at our disposal. We are also grateful to Dr T. S. Allen-Rowlandson, during whose project the animals were collected and who also assisted with the collection of parasites. The technical assistance of Mrs Valerie A. Horak is gratefully acknowledged. We are also indebted to Dr Jane B. Walker for confirming the identities of *R. follis* and *R. lunulatus* and for supplying the appropriate references and to Dr E. M. Nevill for confirming that of *L. paradoxa* and assisting with the identification of the lice.

This research was funded by the Council for Scientific and Industrial Research, the Meat Board and Rhodes University.

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Printed by the Government Printer, Private Bag X85, Pretoria, 0001

Onderstepoort J. vet. Res., 58, 281–284 (1991)

IXODID TICKS AND LICE INFESTING RED DUIKERS AND BUSHPIGS IN NORTH-EASTERN NATAL

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ABSTRACT

HORAK, I. G., BOOMKER, J. & FLAMAND, J. R. B., 1991. Ixodid ticks and lice infesting red duikers and bushpigs in north-eastern Natal. *Onderstepoort Journal of Veterinary Research*, 58, 281–284 (1991)

Eighteen red duikers, *Cephalophus natalensis*, from the Charters Creek Nature Reserve and 2 from Fanies Island Nature Reserve were processed for arthropod parasite recovery. They harboured 8 species of ixodid ticks and 2 lice species. All were infested with *Haemaphysalis parmata* and the nymphs of *Rhipicephalus muehlensi*.

Two bushpigs, *Potamochoerus porcus*, from the Ndumu Nature Reserve, 5 from the Eastern Shores Nature Reserve and 1 from Cape Vidal were examined for ectoparasites. They were infested with 8 ixodid tick species, of which *Rhipicephalus maculatus* was the most abundant, and with 1 louse species.

INTRODUCTION

Red duikers, *Cephalophus natalensis*, are small antelope that are limited to the thick scrub and evergreen forests of the eastern parts of Natal and a small area on the southern slopes of the Soutpansberg in the northern Transvaal (Smithers, 1983). They are considered rare and their status is precarious because of the rapid destruction of their natural habitat (Smithers, 1983). Very little is known about their ecology, but Pienaar (1963) and Heinichen (1972) state that they occur either singly or in temporary pairs, or a female may be accompanied by her offspring. These shy, secretive browsers are found near permanent surface water.

Bushpigs, *Potamochoerus porcus*, are chiefly nocturnal animals that occur in groups, or sounders, of up to 40 individuals. Sounders consist of a dominant board and sow, other sows, juveniles and piglets. They are usually associated with dense vegetation growth, such as forests, thickets, reed beds or heavy cover of tall grass. Like warthogs, bushpigs wallow in mud, probably as a means of temperature regulation and as protection against biting insects. They root in the same way as warthogs, generally making less use of hard ground. In areas where they are hunted, feeding will not commence before late at night but where they are afforded protection, they may be seen in the late afternoon and early morning. They consume a wide variety of plant matter, including fruits, *Acacia* pods and roots, and are known to be attracted to carrion (Smithers, 1983).

The ticks infesting red duikers and bushpigs have been listed by Theiler (1962) and Baker & Keep (1970) and the lice by Ledger (1980). Total tick collections have been made from 3 red duikers in the Charters Creek Nature Reserve (Horak, Keep, Flamand & Boomker, 1988). Two studies on the total numbers of arthropod parasites harboured by warthogs, *Phacochoerus aethiopicus*, have been conducted in southern Africa (Horak, Biggs, Hanssen & Hanssen, 1983; Horak, Boomker, De Vos & Potgieter, 1988), but no such work exists for bushpigs.

The present paper describes the total tick and lice burdens of red duikers and bushpigs examined in the north-eastern Natal nature reserves.

MATERIALS AND METHODS

Survey localities

Charters Creek (28° 14′ S, 32° 25′ E, altitude 0–100 m) and Fanies Island (28° 07′ S, 32° 27′ E, altitude 0–100 m) are nature reserves situated on the western shores of Lake St Lucia. The Eastern Shores Nature Reserve (27° 51′–28° 25′ S, 32° 20′–32° 40′ E, altitude 0–30 m) occupies an area of approximately 250 km^2 at the southern end of the Mozambique coastal plain, between the Indian Ocean to the east and Lake St Lucia to the west. Cape Vidal (28° 08′ S, 32° 33′ E) is a camp situated on the sea shore in the Eastern Shores Nature Reserve, almost opposite Fanies Island.

All these localities form part of the greater St Lucia Nature Reserve, the vegetation of which is classified as the Zululand Palm Veld subdivision of Coastal Thornveld and Coastal communities (Acocks, 1988). The annual rainfall varies between 650 and 1 000 mm, most of which falls in summer. Summers are hot and humid and winters are mild. Frost seldom occurs.

Ndumu Game Reserve (26° 50′–26° 56′ S, 32° 09′–32° 21′ E, altitude 30–100 m) is situated in the extreme north of Natal and comprises an area approximately 11 000 ha in extent. It falls within the Lowveld subtype of Tropical Bush and Savannah (Acocks, 1988). The rainfall varies from 500 to 750 mm *per annum* and falls mostly in summer. Summers are hot and humid and winters are mild. Frost does not occur.

Survey animals

Eighteen red duikers were shot in the Charters Creek Nature Reserve and 2 in the Fanies Island Nature Reserve. Two bushpigs were shot in the Ndumu Nature Reserve, 5 in the Eastern Shores Nature Reserve and 1 at Cape Vidal.

Parasite recovery

The animals were all processed for ectoparasite recovery as described by Horak, Meltzer & De Vos (1982). All the material collected was examined under a stereoscopic microscope and the arthropods collected, identified and counted. The red duikers were also processed for the recovery of helminths and these have been recorded separately (Boomker, Horak & Flamand, 1991).

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Received 19 June 1991—Editor

TABLE 1 Arthropod parasites recovered from 20 red duikers in 2 north-eastern Natal nature reserves

Arthropod species	Total number of arthropods recovered					Number of animals infested
Ixodid ticks	Larvae	Nymphs	Males	Females	Total	
Ambyomma marmoreum	38	8	0	0	46	11
Haemaphysalis leachi	2	0	0	0	2	1
Haemaphysalis parmata	1 388	608	476	116(10)	2 588	20
**Rhipicephalus* spp.	15 194	—	—	—	15 194	20
Rhipicephalus appendiculatus	—	2	2	0	4	2
Rhipicephalus maculatus	—	226	0	0	226	11
Rhipicephalus muehlensi	—	3 246	2	0	3 248	20
Rhipicephalus evertsi evertsi	42	22	0	0	64	2
Rhipicephalus sp. (near *R. oculatus*)	0	0	2	0	2	1
Lice		Nymphs		Adults	Total	
Damalinia sp.		894		398	1 292	9
Linognathus sp.		2 676		1 016	3 692	14

* Undifferentiated larvae of *R. appendiculatus, R. maculatus* and *R. muehlensi,* which are almost indistinguishable when partially engorged

( ) = Number of maturing female ticks that should detach within 24 h, i.e. idiosoma of *H. parmata* > 2,5 mm in length

TABLE 2 Arthropod parasites recovered from 8 bushpigs in 3 north-eastern Natal nature reserves

Arthropod species	Total number of arthropods recovered					Number of animals infested
Ixodid ticks	Larvae	Nymphs	Males	Females	Total	
Amblyomma hebraeum	2	2	6	2	12	3
Haemaphysalis parmata	6	2	0	0	8	1
Rhipicephalus appendiculatus	0	3	2	2	7	2
Rhipicephalus follis	0	0	2	12	14	1
Rhipicephalus maculatus	329	386	2 273	988(54)	3 976	8
Rhipicephalus muehlensi	0	43	0	2	45	3
Rhipicephalus simus	0	0	2	0	2	1
Rhipicephalus zumpti	0	0	81	58(8)	139	6
Lice		Nymphs		Adults	Total	
Haematopinus latus		186		114	300	4

( ) = Number of maturing female ticks that should detach within 24 h, i.e. idiosoma of *R. maculatus* and *R. zumpti* > 6,0 mm in length. The other female ticks had not yet reached this stage of maturation

RESULTS

Red duikers

The animals from the 2 reserves harboured the same parasite species in similar numbers and their burdens have been combined in Table 1.

The red duikers were infested with 8 ixodid tick species of which *Rhipicephalus* spp. larvae (*Rhipicephalus appendiculatus, Rhipicephalus maculatus* and *Rhipicephalus muehlensi*) were the most abundant and, together with all stages of development of *Haemaphysalis parmata* and the nymphs of *R. muehlensi* the most prevalent. No patterns of seasonal abundance could be established because the animals were not shot at regular intervals. Two lice species were also recovered.

Bushpigs

The parasite burdens of the bushpigs from the various localities have been combined and summarized in Table 2.

Eight species of ixodid ticks were recovered. Of these *R. maculatus* was the most abundant and prevalent. Four animals were infested with the louse *Haematopinus latus*.

DISCUSSION

The small size of red duikers and their habitat preference make them ideal hosts for the immature stages of many tick species. Their size also precludes them as hosts for adult ticks of many species as these appear to prefer larger animals (Horak, Potgieter, Walker, De Vos & Boomker, 1983). In contrast bushpigs, like warthogs, carry few immature ticks and are mainly infested by adults (Horak, Boomker, De Vos & Potgieter, 1988). This could be due to host preference or the thickness of their hides or their grooming habits or a combination of all 3 factors.

With the exception of *Amblyomma hebraeum, R. appendiculatus* and *Rhipicephalus simus*, the tick species recovered from the bushpigs differed from those recovered from warthogs in the eastern Transvaal Lowveld (Horak, Boomker, De Vos & Potgieter, 1988). This, however, is related to the geographic distributions of the ticks rather than host preference.

Amblyomma hebraeum: The immature stages of this tick have a particularly wide host range (Theiler, 1962; Horak, MacIvor, Petney & De Vos, 1987). Their virtual absence in the present survey and on common reedbuck, *Redunca arundinum,* examined in the same region (Horak, Keep, Flamand & Boomker, 1988) indicates that these reserves lie on the edge of this tick's distribution in this particular region.

Amblyomma marmoreum: The adults feed almost exclusively on tortoises, while the immature stages can be found on many host species (Theiler, 1962; Norval, 1975; Horak, MacIvor, Petney & De Vos, 1987). The small numbers on the red duikers are thus not unexpected.

Haemaphysalis parmata: The immature stages are not easily distinguishable from those of *Haemaphysalis silacea,* which also occurs in this region (Horak, Keep, Flamand & Boomker, 1988). Because we recovered the adults of only *H. parmata* in the present survey we have assigned the immature stages to this species as well.

Theiler (1962) states that *H. parmata* is a central and west African tick that ranges into the forested highlands of eastern Africa. She questions whether the only record for South Africa that she lists from Durban may not be due to a recent introduction. Horak, Keep, Flamand & Boomker (1988) surmised that it was more widespread than Theiler had thought and the present results confirm this. They felt that the bushbuck was a favoured host of this species, and red duikers must now also fall within this category.

Rhipicephalus appendiculatus: Very few ticks of this species were recovered from common reedbuck in the Eastern Shores Nature Reserves, but fairly large numbers were present on these animals in the Charters Creek Reserve (Horak, Keep, Flamand & Boomker, 1988). Their virtual absence on the red duikers and bushpigs in the present survey could be due either to host preference or to the very dense vegetation both species prefer as habitat.

Rhipicephalus follis: Although this tick is fairly widespread in the eastern half of the country (Horak, Keep, Spickett & Boomker, 1989; Horak, Fourie, Novellie & Williams, 1991), with the possible exception of eland, it is never encountered in large numbers (Horak *et al.*, 1991). Only 1 of the bushpigs was infested.

Rhipicephalus maculatus: Buffaloes appear to be the preferred hosts of all stages of development (Horak *et al.*, 1983). The immature stages may also be found on red duikers, nyala, *Tragelaphus angasi,* and bushpigs (Baker & Keep, 1970; Horak, Potgieter, Walker, De Vos & Boomker, 1983). Judging by the present findings, the latter animals are also excellent hosts of the adults.

Rhipicephalus muehlensi: Nyala are the preferred hosts of all stages of development (Horak, Potgieter, Walker, De Vos & Boomker, 1983). Red duikers, probably because they share the nyalas' habitat, may harbour large numbers of immatures. Even though bushpigs share the same habitat they harbour few specimens of this species.

Rhipicephalus simus prefers monogastric animals such as zebras, carnivores and warthogs (Horak, De Vos & De Klerk, 1984; Horak, Jacot Guillarmod, Moolman & De Vos, 1987; Horak, Boomker, De Vos & Potgieter, 1988). The small number recovered from only 1 of the bushpigs is probably more a reflection of the tick's geographic distribution than host preference.

Rhipicephalus zumpti: Baker & Keep (1970) have recorded this tick from black rhinoceros in Natal. According to them it is prevalent in Mozambique, but rare in Zululand. However, Clifford & Anastos (1962) have synonymized *R. zumpti* with *Rhipicephalus reichenowi*, which in turn has been synonymized with *Rhipicephalus planus* (Morel, 1980). Nevertheless it may yet prove to be a valid species. The presence of *R. zumpti* on 6 of the 8 bushpigs not only indicates that they are preferred hosts, but that the tick might not be rare in the north-eastern regions of Natal and Zululand.

No specific identifications of the lice on the red duikers were made. *Damalinia* species have not previously been recorded from this host (Ledger, 1980). The *Linognathus* species recovered seemed to belong to the *L. breviceps* group, but there is controversy concerning the identities of lice belonging to this group (Ledger, 1980). *Haematopinus latus,* recovered from the bushpigs, fairly closely resembles *Haematopinus phacochoeri* which parasitizes warthogs (Ledger, 1980).

ACKNOWLEDGEMENTS

We wish to thank the Natal Parks Board for placing the red duikers and bushpigs at our disposal and for supplying the staff and facilities for processing the animals for parasite recovery.

We are most grateful for the technical assistance of Mrs Santa Meyer, Miss Renade Bartlett and Mr E. J. Williams. Dr Jane B. Walker assisted with the identification of *R. zumpti* and also supplied the references concerning this species.

This research was funded by the Foundation for Research Development.

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Printed by the Government Printer, Private Bag X85, Pretoria, 0001

Onderstepoort J. vet. Res., 59, 253–257 (1992)

ARTHROPOD PARASITES OF SPRINGBOK, GEMSBOK, KUDUS, GIRAFFES AND BURCHELL'S AND HARTMANN'S ZEBRAS IN THE ETOSHA AND HARDAP NATURE RESERVES, NAMIBIA

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ABSTRACT

HORAK, I. G., ANTHONISSEN, M., KRECEK, R. C. & BOOMKER, J., 1992. Arthropod parasites of springbok, gemsbok, kudus, giraffes and Burchell's and Hartmann's zebras in the Etosha and Hardap Nature Reserves, Namibia. *Onderstepoort Journal of Veterinary Research*, 59, 253–257 (1992)

A total of 48 springbok, 48 gemsbok, 23 kudus and 6 giraffes were examined for ticks and lice, while 9 Burchell's zebras and 6 Hartmann's mountain zebras were examined only for ticks. Springbok and gemsbok were shot in both the Etosha National Park in the north and the Hardap Nature Reserve in the south of Namibia. All the other animals were shot in the Etosha National Park.

A total of 7 ixodid tick species and 8 lice species were recovered. The springbok carried few ticks. The adults of a *Rhipicephalus* sp. (near *R. oculatus*) were most numerous on the gemsbok, especially during November. The kudus were the only animals harbouring *Rhipicephalus zambeziensis*. Adult *Hyalomma truncatum*, followed by adult *Hyalomma marginatum rufipes*, were most abundant on the giraffes and adult *Rhipicephalus evertsi mimeticus* were commonest on the zebras.

INTRODUCTION

The ixodid ticks found in Namibia have been listed by Theiler (1962). Her records were compiled after the identification of ticks that had generally been collected by stock inspectors, veterinarians, zoologists and other interested parties. These did not represent total collections of ticks from the animals examined.

In recent times more thorough collections of ticks have been made by examining animals of a particular species at regular intervals for periods of at least 1 year. Warthogs (*Phacochoerus aethiopicus*), Hartmann's mountain zebras (*Equus zebra hartmannae*) and cattle have been examined in Namibia in this way and 9 ixodid tick species recovered (Horak, Biggs, Hanssen & Hanssen, 1983; Horak, Biggs & Reinecke, 1984; Biggs & Langenhoven, 1984). In a recent review of ticks occurring in southern Africa, Walker (1991) lists 30 species from Namibia.

A number of animals of various species were to be shot in the Etosha National Park and the Hardap Nature Reserve, Namibia, for reproductive and biological studies, while others were to be killed for helminth recovery. This presented the opportunity to obtain ticks also from these animals and collections were made from springbok (*Antidorcas marsupialis*), gemsbok (*Oryx gazella*), kudus (*Tragelaphus strepsiceros*), giraffes (*Giraffa camelopardalis angolensis*), Burchell's zebras (*Equus burchelli antiqorum*) and Hartmann's mountain zebras. This paper records the ixodid tick burdens of these animals, and the lice burdens of the springbok, gemsbok and kudus. The helminths from the zebras, kudus and giraffes have been reported elsewhere (Krecek, Reinecke & Malan, 1987; Boomker, Anthonissen & Horak, 1988; Krecek, Boomker, Penzhorn & Scheepers, 1990).

MATERIALS AND METHODS

Study sites

The localities at which the animals were shot are summarized in Table 1.

Survey animals

Springbok and gemsbok were shot in the Hardap Nature Reserve at approximately 2-monthly intervals from May 1983 to June 1984. Springbok were also shot near Okaukuejo and gemsbok from near Otjovasandu in the Etosha National Park from June 1983 until April 1984 and February 1984 respectively. In addition 4 gemsbok were shot near Okaukuejo towards the end of April and beginning of May 1984. Kudus were shot at 2-monthly intervals near Namutoni, Etosha National Park, from June 1983 until April 1984. Nine Burchell's zebras and 6 Hartmann's mountain zebras were shot near Okaukuejo and Otjovasandu respectively in the Etosha National Park.

Two giraffes were shot near Okaukuejo in November 1985, 2 in March 1986 and 2 in July 1986. These months fall within the 3 seasons described for Etosha by Berry (1980); these are hot and wet (January to April); cold and dry (May to August), and hot and dry (September to December).

Parasite recovery

The springbok, gemsbok, kudus and giraffes were processed for ectoparasite recovery as described by Horak, Boomker, Spickett & De Vos (1992). Ticks were recovered from the zebras by making whole body searches; this meant that few immature ticks and no lice were collected. The ectoparasites from all the animals were identified and counted under a stereoscopic microscope.

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Received 12 August 1992—Editor

TABLE 1 Localities at which various herbivores were shot in Namibia for the recovery of arthropod parasites

Locality	Co-ordinates	Vegetation type (Van der Merwe, 1983)
Otjovasandu, Etosha National Park	19° 15′ S, 14° 30′ E	Mopane savanna
Okaukuejo, Etosha National Park	19° 11′ S, 15° 55′ E	Mopane savanna
Namutoni, Etosha National Park	18° 49′ S, 16° 56′ E	Saline desert with dwarf shrub savanna fringe surrounded by Mopane savanna and Forest savanna and woodland
Hardap Nature Reserve	24° 30′ S, 17° 45′ E	Dwarf shrub savanna

TABLE 2 Ixodid ticks recovered from various wild herbivores in Namibia

Tick and host species	Locality	No. examined	No. infested	No. of ticks recovered				
				Larvae	Nymphs	Males	Females	Total
Hyalomma marginatum rufipes								
Gemsbok	Otjovasandu	18	1	0	0	1	0	1
	Okaukuejo	4	2	0	0	9	1	10
	Hardap	26	1	0	0	4	0	4
Giraffe	Okaukuejo	6	6	0	0	372	75	447
Burchell's zebra	Okaukuejo	9	3	0	0	8	1	9
Hartmann's mountain zebra	Otjovasandu	6	3	0	0	10	5	15
Hyalomma truncatum								
Gemsbok	Otjovasandu	18	5	0	0	6	1	7
	Okaukuejo	4	2	0	0	12	8	20
	Hardap	26	1	0	0	2	0	2
Giraffe	Okaukuejo	6	6	0	0	1550	584	2134
Burchell's zebra	Okaukuejo	9	1	0	0	2	0	2
Hartmann's mountain zebra	Otjovasandu	6	5	0	0	27	1	28
Rhipicephalus evertsi mimeticus								
Springbok	Okaukuejo	21	1	1	0	0	0	1
	Hardap	27	1	6	0	0	0	6
Gemsbok	Otjovasandu	18	2	0	3	2	0	5
Kudu	Namutoni	23	18	4835	1057	23	23	5938
Giraffe	Okaukuejo	6	5	0	0	14	5	19
Burchell's zebra	Okaukuejo	9	6	5	4	34	9	52
Hartmann's mountain zebra	Otjovasandu	6	5	13	9	46	13	81
Rhipicephalus longiceps								
Giraffe	Okaukuejo	6	1	0	0	1	0	1
Rhipicephalus turanicus								
Burchell's zebra	Okaukuejo	9	1	0	0	0	1	1
***Rhipicephalus sp.* (near *R. oculatus*)**								
Springbok	Hardap	27	4	0	0	3	1	4
Gemsbok	Otjovasandu	18	1	0	0	1	0	1
	Hardap	26	17	0	0	220	130	350
Kudu	Namutoni	23	6	0	0	10	4	14
Rhipicephalus zambeziensis								
Kudu	Namutoni	23	7	2	0	10	8	20

RESULTS AND DISCUSSION

Ixodid ticks

The tick species recovered, the hosts from which they were collected and the localities at which the hosts were examined are summarized in Table 2.

A total of 7 ixodid tick species were recovered. With the exception of the *Rhipicephalus* sp. (near *R. oculatus*), the Etosha National Park seemed to be a more favourable habitat for all species than the Hardap Nature Reserve. As noted in previous surveys, springbok had very low tick burdens (Horak, Meltzer & De Vos, 1982; De Villiers, Liversidge & Reinecke, 1985; Horak, Fourie, Novellie & Williams, 1991). Whether this was due to natural immunity, or host preference, or habitat preference, or behaviour of the antelope could not be determined in either this or the other surveys.

Hyalomma spp.

Both *Hyalomma marginatum rufipes* and *Hyalomma truncatum* prefer the drier western regions of southern Africa (Theiler, 1962; Howell, Walker & Nevill, 1978; Walker, 1991). Judging by the present results the Okaukuejo region of the Etosha National Park is a better habitat for *H. truncatum* than for *H. marginatum rufipes*. The preferred hosts of the adults are large animals such as cattle (Horak, 1982; Biggs & Langenhoven, 1984), horses (Horak, Biggs & Reinecke, 1984; Horak, Knight & De Vos, 1986), zebras and eland (Rechav, Zeederberg & Zeller, 1987; Horak *et al.*, 1991). The present results indicate that giraffes probably rank above all the other animals mentioned above as the host of choice. Each of the 6 giraffes examined harboured more than 200 adult *Hyalomma* and 1 of them more than 850 ticks.

Kudus are definitely not good hosts of adult *H. truncatum* (Horak *et al.,* 1992), while gemsbok should only be considered fair hosts of both species (Fourie, Vrahimis, Horak, Terblanche & Kok, 1991). Warthogs examined in the northern bushveld region of Namibia harboured more *H. truncatum* than *H. marginatum rufipes* (Horak *et al.,* 1983), while the converse was true for mountain zebras and horses examined in the central region west of Windhoek, and cattle examined east of Windhoek (Horak *et al.,* 1984; Biggs & Langenhoven, 1984). The preferred hosts of the immature stages of both species are scrub hares (Rechav *et al.,* 1987; Horak *et al.,* 1991; Horak & Fourie, 1991).

As only 2 giraffes were examined on each occasion, and then at 4-monthly intervals, it is virtually impossible to determine a pattern of seasonal abundance for these ticks. The total counts of *H. marginatum rufipes* were 206, 189 and 52, and those of *H. truncatum* 497, 602 and 1035, for both animals examined during November 1985 and March and July 1986 respectively.

Both these ticks have long mouthparts and these can cause considerable tissue damage, which may lead to secondary bacterial infection (Howell *et al.,* 1978). *H. marginatum rufipes* is a vector of *Anaplasma marginale*, the cause of gallsickness in cattle (Potgieter, 1981), and *H. truncatum* transmits a toxin causing sweating sickness in the latter animals (Howell *et al.*, 1978).

Rhipicephalus evertsi mimeticus

We are unable to differentiate the immature stages of this tick from those of *Rhipicephalus evertsi evertsi*. However, as the adults of only *R. evertsi mimeticus* were recovered we have assigned all the immatures to this subspecies. This tick prefers the arid regions of Namibia and western Botswana (Howell *et al.*, 1978).

In the case of *R. evertsi evertsi* equids are among the preferred hosts of all stages of development (Norval, 1981; Horak *et al.*, 1986). *R. evertsi mimeticus* appears also to favour these hosts (Horak *et al.*, 1984). The collection methods employed on the zebras in the present survey virtually precluded the recovery of immature ticks, which are found in the outer ear canals, and the numbers of adult ticks recovered were also small. Nevertheless their mean burdens of adult ticks were slightly higher than those of the other host species. The vast majority of the immature ticks recorded from the kudus at Namutoni were found on a single animal, which carried 4 172 larvae and 952 nymphs. Kudus are considered to be poor hosts of the closely related *R. evertsi evertsi* (Horak *et al.*, 1992).

No pattern of seasonal abundance was evident.

Rhipicephalus longiceps

Walker (1991) cites this as a rare tick found only in Namibia and Angola. It has been recovered from cattle, klipspringer and gemsbok (Walker, 1991), also from 3 of 37 warthogs examined in the northern bushveld of Namibia (Horak *et al.*, 1983). Its recovery from one of the giraffes appears to constitute a new host record.

Rhipicephalus turanicus

This tick has previously been recovered in the Etosha National Park and from Grootfontein in northern Namibia (Walker, 1991). Its adults have a very wide host range, and amongst the wild animals ostriches and zebras appear to carry the largest numbers (Pegram, Clifford, Walker & Keirans, 1987).

Rhipicephalus sp. (near *R. oculatus*)

The problems surrounding the species diagnosis of this tick and *Rhipicephalus oculatus sensu stricto* have been discussed by Walker (1991). She also records it as being widely distributed in Namibia, especially south of Windhoek, an observation confirmed by the present findings.

Walker (1991) lists the wild hosts as being mostly antelopes, particularly gemsbok and kudus. It has also been recorded (as *R. oculatus*) from 7 of 37 warthogs examined in the northern bushveld region of Namibia (Horak *et al.,* 1983). In the present survey gemsbok were more heavily infested than kudus, possibly owing to the more southerly locality at which they were examined. In a recent survey in South Africa, kudus just north of Grahamstown, in the eastern Cape Province, were more heavily infested than sheep, goats, cattle and scrub hares from the same locality (Horak & Knight, 1986).

No clear pattern of seasonal abundance could be seen on the eastern Cape kudus, but no ticks of this species were present on the animals examined during May and June (Horak *et al.,* 1992). The scrub hares from that particular locality, however, generally carried larger numbers of adult ticks during August and from November to April (Horak & Fourie, 1991). In the present survey the gemsbok in the Hardap Nature Reserve harboured the greatest numbers of ticks during November and February (Fig. 1). The largest numbers of ticks (a total of only 6 on 4 animals) were recorded on the kudus in the Etosha National Park during June and during August.

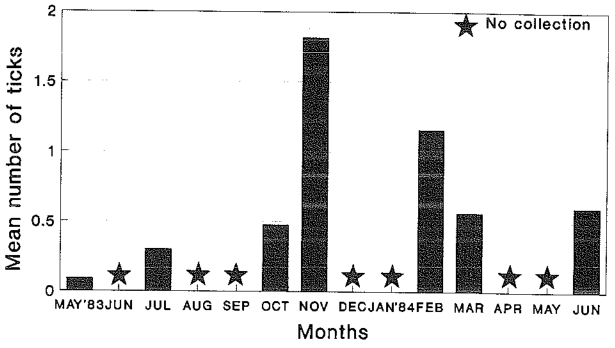

FIG. 1 The seasonal abundance of a *Rhipicephalus* sp. (near *R. oculatus*) on gemsbok in the Hardap Nature Reserve, Namibia [$\log_{10}$ (x + 1)]

Rhipicephalus zambeziensis

This tick has been recorded in northern Namibia in the Kunene (Kaokoland) and the Otjozondjupa (Grootfontein) districts (Norval, Walker & Colborne, 1982). Namutoni, in the Etosha National Park, lies between these 2 regions. *R. zambeziensis* infests a large variety of hosts, including carnivores, suids and bovids (Walker, 1991). Within its distribution range kudus appear to be amongst the preferred hosts of all stages of development (Horak *et al.,* 1992).

R. zambeziensis can transmit *Theileria parva parva* and *Theileria parva bovis,* the cause of East Coast fever and January disease respectively in cattle (Lawrence, Norval & Uilenberg, 1983). It also transmits *Theileria parva lawrencei* to buffaloes and cattle. In the former animals *T. parva lawrencei* is not pathogenic, but it produces the usually fatal Corridor disease in cattle.

Lice

The springbok harboured the greatest number of lice species, but the total burdens of individual animals were low (Table 3). No pattern of seasonal abundance was evident. De Villiers *et al.,* (1985) examined springbok near Kimberly in the Cape Province, South Africa, for parasites at fairly regular intervals for a period of 14 months. They recovered 6 lice species from these animals and the 4 major species all exhibited peak burdens during September.

TABLE 3 Lice recovered from springbok, gemsbok and kudus in Namibia

Host and lice species	Number of hosts examined	Number infested	Number of lice recovered		
			Nymphs	Adults	Total
Springbok					
Damalinia antidorcus	48	8	3	16	19
Linognathus antidorcitis	48	23	45	43	88
Linognathus armatus	48	1	0	11	11
Linognathus bedfordi	48	1	3	2	5
Linognathus euchore	48	15	35	40	75
Gemsbok					
Haematopinus oryx	48	3	38	5	43
Linognathus oryx	48	28	3567	737	4304
Kudu					
Linognathus taurotragus	23	17	582	311	893

Two lice species were recovered from the gemsbok, of which *Linognathus oryx* was the most abundant. The seasonal abundance of the latter species on the gemsbok is illustrated in Fig. 2.

Lice numbers started to increase sooner on the animals in the Hardap Reserve than on those in the Etosha Park. Peak numbers were recorded during November and December respectively (summer).

In contrast peak burdens of the louse *Linognathus taurotragus* were recorded in June (winter) on the kudus examined at Namutoni in the Etosha National Park (Fig. 3). No lice were recovered from the giraffes.

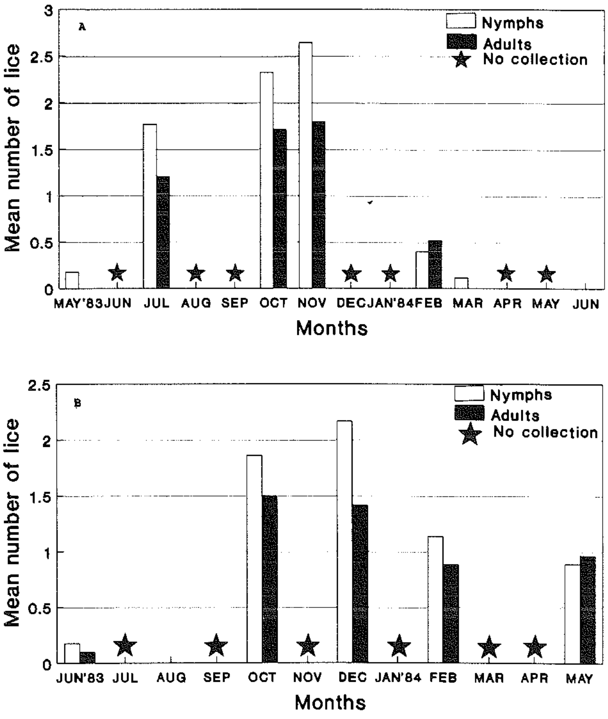

FIG. 2 The seasonal abundance of *Linognathus oryx* on gemsbok in Namibia [$\log_{10}(x + 1)$]

A. in the Hardap Nature Reserve

B. in the Etosha National Park

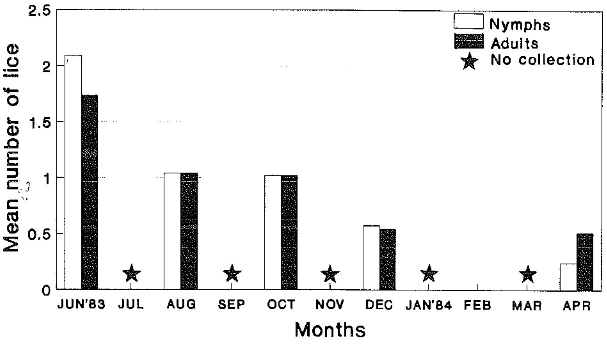

FIG. 3 The seasonal abundance of *Linognathus taurotragus* on kudus in the Etosha National Park, Namibia [$\log_{10}(x + 1)$]

ACKNOWLEDGEMENTS

This study is part of the Wildlife Research Programme of the Faculty of Veterinary Science, University of Pretoria.

We would like to thank the Director, Department of Agriculture and Nature Conservation, for placing the animals at our disposal and Dr H. C. Biggs, Central Veterinary Laboratory, Windhoek for making the necessary arrangements, and the staff of the 2 nature reserves for their assistance with the necropsies. Messrs L. Scheepers and T. E. Krecek assisted with the parasite recoveries from the giraffes and Mrs Bonnie Roper, Prof. R. K. Reinecke and Dr F. S. Malan with those from the zebras. Mrs Santa Meyer collected the arthropod parasites from the processed material. Dr Jane B. Walker assisted with the identification of *R. longiceps*. Miss Andrea van Niekerk drew the graphs.

This research was funded by the Foundation for Research Development and the University of Pretoria.

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PARASITES OF DOMESTIC AND WILD ANIMALS IN SOUTH AFRICA. XXX. ECTOPARASITES OF KUDUS IN THE EASTERN TRANSVAAL LOWVELD AND THE EASTERN CAPE PROVINCE

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ABSTRACT

HORAK, I. G., BOOMKER, J., SPICKETT, A. M. & DE VOS, V., 1992. Parasites of domestic and wild animals in South Africa. XXX. Ectoparasites of kudus in the eastern Transvaal Lowveld and the eastern Cape Province. *Onderstepoort Journal of Veterinary Research*, 59, 259–273 (1992)

Sets of four kudus were shot and examined for arthropod parasites at approximately monthly intervals from April 1981 to March 1983 in the southern part of the Kruger National Park, eastern Transvaal Lowveld. These animals harboured 10 ixodid tick species of which *Boophilus decoloratus* followed by *Amblyomma hebraeum* were the most abundant. The seasonal abundances of these ticks and of *Amblyomma marmoreum, Rhipicephalus appendiculatus, Rhipicephalus evertsi evertsi* and *Rhipicephalus zambeziensis* were determined. The kudus were also infested with 3 lice and 1 louse fly species, as well as the nymphs of a pentastomid.

Sixteen kudus were shot in the Andries Vosloo Kudu Reserve, eastern Cape Province and 9 on an adjacent farm. These animals were infested with 12 tick species. *A. hebraeum* followed by *Rhipicephalus glabroscutatum* were the most abundant on kudus in the reserve and *R. glabroscutatum* followed by *Haemaphysalis silacea* on the animals on the farm. The seasonal abundances of *A. hebraeum, A. marmoreum, H. silacea, R. appendiculatus, R. glabroscutatum* and a *Rhipicephalus* sp. (near *R. oculatus*) were determined on the kudus in the reserve. The kudus were also infested with 3 lice and 1 louse fly species. Two kudus examined in the Addo Elephant National Park were infested with 6 tick, 1 louse and 1 louse fly species.

INTRODUCTION

A number of surveys on the abundance of ectoparasites on a variety of host species have already been conducted in the eastern Transvaal Lowveld and the eastern Cape Province. Blue wildebeest, Burchell's zebras, warthogs and helmeted guineafowls have been examined in the Kruger National Park, eastern Transvaal Lowveld (Horak, De Vos & Brown, 1983; Horak, De Vos & De Klerk, 1984; Horak, Boomker, De Vos & Potgieter, 1988; Horak, Spickett, Braack & Williams, 1991). While kudus, cattle, Dorper sheep, Angora goats, scrub hares and helmeted guineafowls have been examined in the Andries Vosloo Kudu Reserve and/or on the adjacent farm "Bucklands", eastern Cape Province (Knight & Rechav, 1978; Rechav, 1982; Horak, Williams & Van Schalkwyk, 1991; Horak, Spickett, Braack & Williams, 1991; Horak, Knight & Williams, 1991; Horak & Fourie, 1991).

Several studies on the ixodid tick burdens of kudus, *Tragelaphus strepsiceros,* have been published. Knight & Rechav (1978) examined 25 animals from the farms "Bucklands" and "Ulster" and Horak, Potgieter, Walker, De Vos & Boomker (1983) 4 animals in the Kruger National Park and 5 from the Andries Vosloo Kudu Reserve. Horak & Knight (1986) and Petney & Horak (1987) also compared the burdens of some of the animals from the Andries Vosloo Kudu Reserve, included in the present paper, with those of kudus on the adjacent farm "Bucklands". These surveys all indicate that kudus are good hosts of several tick species and may become heavily infested, a fact also commented on by Lightfoot & Norval (1981) in Zimbabwe.

Kudus are large antelope that are widely distributed in southern and East Africa. They prefer light forest or dense bush (Ansell, 1971) and generally avoid open country (Dorst & Dandelot, 1972; Rautenbach, 1982). They usually live in small groups comprising adult cows and their offspring. Calves remain hidden for approximately the first 3 months of life and then join the cow groups (Novellie, 1983). Male animals leave the group when about 2 years old, while females stay with the group until fully mature (Novellie, 1983). Adult bulls form bachelor groups that join the cows during the breeding season (Novellie, 1983).

The present paper describes surveys on the abundance of ectoparasites of kudus shot in the Kruger National Park, eastern Transvaal Lowveld, in the Andries Vosloo Kudu Reserve and on the adjacent farm "Bucklands", and in the Addo Elephant National Park, eastern Cape Province. The kudus in these surveys were also examined for internal parasites and this has been reported elsewhere (Boomker, Horak & De Vos, 1989; Boomker, Horak & Knight, 1991).

MATERIALS AND METHODS

Parasite recovery

After the animals had been shot they were transported to the laboratories at Skukuza in the Kruger National Park or Grahamstown in the eastern Cape Province. There the carcass of each animal was skinned and half the skin of the head, half the skin of the body and upper legs, the whole skin of the tail as well as 1 lower front leg and 1 lower back leg with skin attached were placed separately in plastic bags. A tick-detaching agent[1] was added

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Received 15 July 1992—Editor

[1] Triatix: Coopers South Africa (Pty) Ltd

TABLE 1 Arthropod parasites of 95 kudus in the Kruger National Park

Arthropod species	Total number recovered					No. of kudus infested
Ixodid ticks	Larvae	Nymphs	Males	Females	Total	
Amblyomma hebraeum	67 216	9 801	659	291(9)	77 967	95
Amblyomma marmoreum	465	0	0	0	465	18
Boophilus decoloratus	161 815	107 711	35 959	18 140(360)	323 625	95
Haemaphysalis leachi/spinulosa	1	0	0	0	1	1
Hyalomma truncatum	0	0	30	6	36	16
Ixodes sp.	2	1	0	0	3	2
Rhipicephalus appendiculatus	11 915	3 208	3 062	1 721(31)	19 906	88
Rhipicephalus evertsi evertsi	9 015	940	167	63(2)	10 185	92
Rhipicephalus simus	0	0	6	9	15	5
Rhipicephalus zambeziensis	14 365	2 062	963	485(7)	17 875	91
Lice	Nymphs		Adults		Total	
Damalinia sp.	4 336		2 375		6 711	73
Haematopinus taurotragi	470		413		883	23
Linognathus taurotragus	4 782		2 781		7 563	43
Louse flies	Adults				Total	
Lipoptena paradoxa	4 616				4 616	94
Pentastomids	Nymphs				Total	
Linguatula nuttalli	667				667	60

( ) = Number of maturing females i.e. idiosoma of *A. hebraeum* >9,5 mm; *B. decoloratus* >4,0 mm; *R. appendiculatus* >5,0 mm; *R. evertsi evertsi* >6,0 mm; *R. zambeziensis* >5,0 mm. Females of the other tick species had not started to mature

to the skins in the bags which were tightly secured and stored overnight. The following morning the skins were thoroughly scrubbed with brushes with steel bristles and washed. The tick-detaching agent remaining in the plastic bags and the material obtained from scrubbing and washing the skins were sieved on sieves with 0,15 mm apertures. The residues in the sieves were collected, preserved in 10 % formalin and stored.

Pentastomid nymphs were recovered from the hearts, livers and lungs of the kudus, which had all been processed for helminth recovery (Boomker *et al.*, 1989).

Parasite counts

Representative samples of the material collected were examined under a stereoscopic microscope, and the parasites identified and counted. The remainder of the material was examined macroscopically for the presence of adult ticks and louse flies. These and the pentastomid nymphs recovered from the hearts, livers and lungs were counted and identified under a stereoscopic microscope. The data on the louse flies will be reported separately.

SURVEYS AT PARTICULAR LOCALITIES

Kruger National Park (KNP)

Study site

This has been described in some detail by Boomker *et al.* (1989). In summary, it is located in the southern part of the park between latitude 25° 06′–25° 21′ S and longitude 31° 27′–31° 36′ E. The vegetation is classified as Lowveld (Acocks, 1988). The days are warm to hot in summer and mild in winter and frost occurs occasionally. Rainfall varies from 600–700 mm per annum and usually falls in summer.

Survey animals

Each month from April 1981 to March 1983, 4 kudus were shot in the study area. At each occasion an attempt was made to obtain 1 adult male, 1 adult female, 1 young or sub-adult male and 1 calf of either sex. The animals were aged according to Simpson (1971). For statistical reasons they have been grouped according to age into calves (0–12 months old), juveniles (13–24 months old), young adults (25–48 months old) and prime or old adults (49 months and older). A total of 96 kudus were shot, but only 95 were examined for ectoparasites as the material collected from 1 had not been adequately preserved.

Arthropod burdens

The total numbers of arthropod parasites recovered from the kudus shot in the survey area are summarized in Table 1.

The animals were infested with 10 ixodid tick species. *Boophilus decoloratus* and *A. hebraeum* were the most abundant and all kudus were infested. They were also infested with 3 lice and 1 louse fly species.

Seasonal abundance

The seasonal abundances of *A. hebraeum, Amblyomma marmoreum, B. decolaratus, Rhipicephalus appendiculatus, Rhipicephalus evertsi evertsi* and *Rhipicephalus zambeziensis* on the kudus are graphically illustrated in Fig. 1.

A. hebraeum exhibited no clear pattern of seasonal abundance, while the larvae of *A. marmoreum* were consistently present from March to July 1982 and during February and March 1983. Peak burdens of *B. decoloratus* were recorded in September and October 1981, and November and December

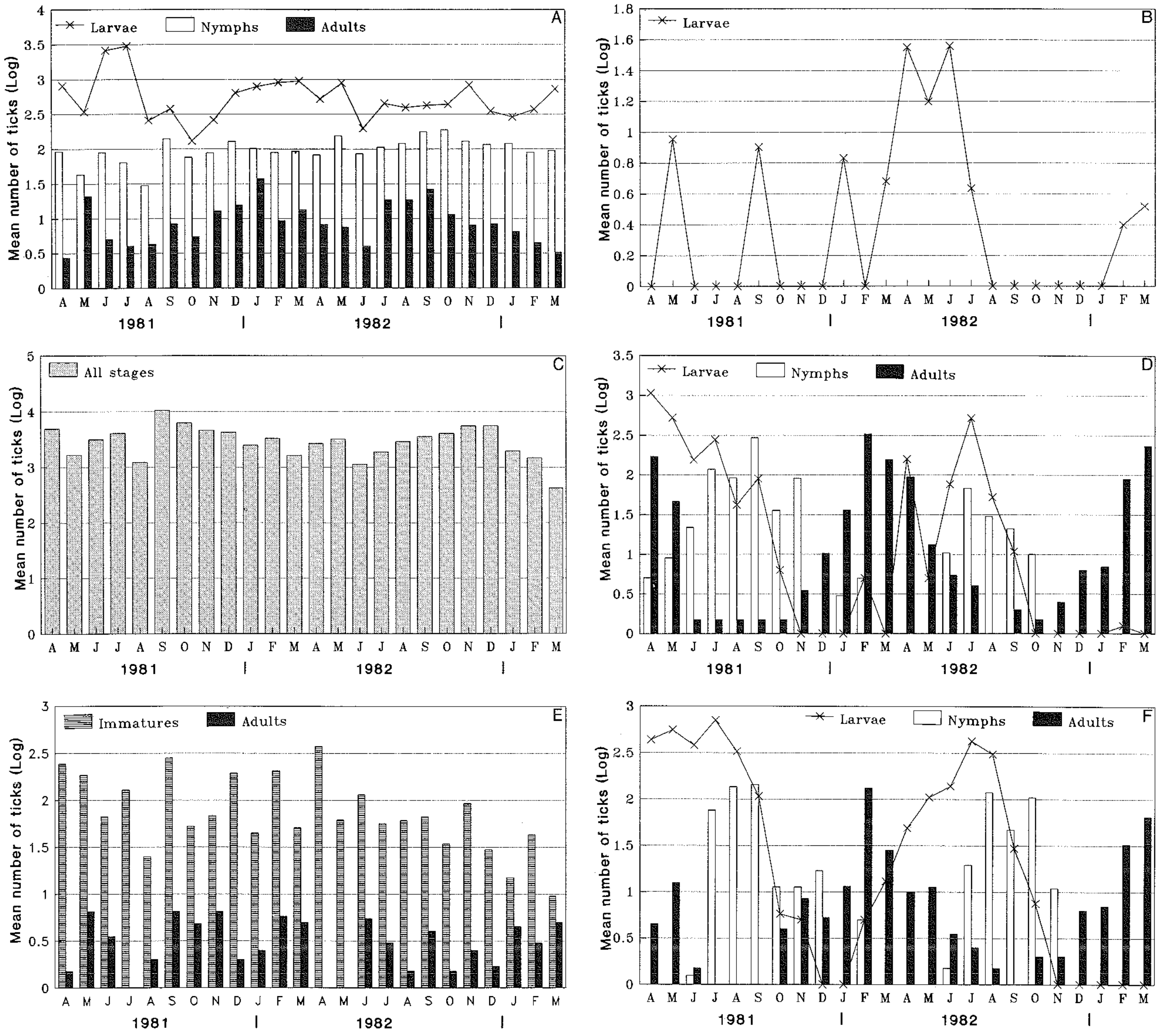

FIG. 1 The seasonal abundance of
A. *Amblyomma hebraeum,* B. *Amblyomma marmoreum,* C. *Boophilus decoloratus,* D. *Rhipicephalus appendiculatus,* E. *Rhipicephalus evertsi evertsi* and F. *Rhipicephalus zambeziensis* on kudus in the Kruger National Park

1982. The larvae of *R. appendiculatus* reached the largest numbers from April to July, the nymphs from July to September or November, and the adults during February to April. No clear pattern of seasonal abudance was evident for *R. evertsi evertsi.* Large numbers of larvae of *R. zambeziensis* were present from April to September, nymphs from July to September or October and adults during February and March.

Host sex-preferences

The host sex-preferences of *A. hebraeum* and *B. decoloratus* are summarized in Table 2.

Adult male kudus harboured significantly more nymphs, males and females of *A. hebraeum,* and more males and females of *B. decoloratus* than adult female animals. No such differences were noted for the other tick species or between adult animals and calves of 6 months or less of age.

Andries Vosloo Kudu Reserve (AVKR) and the farm "Bucklands"

Study site

The reserve (6 497 ha in extent) and the farm (5 480 ha), share an 11 km common boundary, and are situated in the eastern Cape Province around 33° 07 ′ S and 26° 40′ E with altitudes ranging from 335–538 m. The vegetation is classified as Valley Bushveld (Acocks, 1988). Rainfall is non-seasonal and the long-term mean annual total is 484 mm of which slightly more than 300 mm falls from October to March.

At the time of the survey the reserve contained approximately 450 kudus, 54 hartebeest, 140 eland and 100 buffaloes, and the farm approximately 300 kudus, 300 Dorper sheep, 4 000 Angora goats and 185 cattle. The domestic stock were regularly treated with an acaricide. Both properties harboured

TABLE 2 A comparison of the burdens of *Amblyomma hebraeum* and *Boophilus decoloratus* of 15 adult male and 15 adult female kudus shot in pairs during the same months and in the same locality, using a Wilcoxon matched-pairs signed-ranks test

Tick species	Developmental stage	Mean number of ticks recovered from adult kudus		Wilcoxon T value	Significance P =
		Male kudus	Female kudus		
Abmlyomma hebraeum	Nymphs	144,7	103,2	20,0	0,050
	Males	22,1	2,8	0,0	0,001
	Females	11,1	0,5	0,0	0,001
Boophilus decoloratus	Males	503,7	338,2	24,0	0,050
	Females	302,3	154,2	15,0	0,050

TABLE 3 Arthropod parasites of 16 kudus in the Andries Vosloo Kudu Reserve

Arthropod species	Total number recovered					No. of kudus infested
Ixodid ticks	Larvae	Nymphs	Males	Females	Total	
Amblyomma hebraeum	32 009	3 568	464	252(22)	36 293	16
Amblyomma marmoreum	2 112	0	0	0	2 112	11
Boophilus decoloratus	8	36	34	20	98	5
Haemaphysalis silacea	10 003	2 309	1 410	415(66)	14 137	16
Hyalomma marginatum rufipes	0	0	3	0	3	1
Hyalomma truncatum	0	0	2	0	2	1
Ixodes pilosus	0	14	2	12	28	4
Rhipicephalus appendiculatus	4 391	775	334	180(24)	5 680	16
Rhipicephalus evertsi evertsi	296	145	18	10	469	16
Rhipicephalus glabroscutatum	13 596	7 269	1 043	544(20)	22 452	16
Rhipicephalus sp. (near *R. oculatus*)	0	0	104	41(14)	145	13
Rhipicephalus simus	0	0	2	4	6	2
Lice	Nymphs		Adults		Total	
Haematopinus taurotragi	486		92		578	4
Linognathus taurotragus	1 895		784		2 679	16
Louse flies	Adults				Total	
Lipoptena paradoxa	108				108	13

( ) = Number of maturing females i.e. idiosoma of *A. hebraeum* >9,5 mm; *H. silacea* >5,0 mm; *R. appendiculatus* >5,0 mm; *R. glabroscutatum* >4,0 mm; *Rhipicephalus* sp. (near *R. oculatus*) >5,0 mm in length. Females of the other tick species had not started to mature

large numbers of small antelope, scrub hares and helmeted guineafowls.

Survey animals

Each month, from February 1985 to January 1986, and every 3 months thereafter, commencing March 1986 until December 1986, a single adult male kudu was shot on the reserve. With the exception of June 1985 when 2 kudus were shot, 1 adult male kudu was shot on "Bucklands" every 3 months from March 1985 until December 1986. In this way 16 kudus on the reserve and 9 kudus on the farm where shot and examined.

Arthropod burdens

The total numbers of arthropod parasites recovered from kudus on the reserve and on the farm are summarized in Tables 3 and 4 respectively.

The kudus on the reserve were infested with 12 ixodid tick species of which *A. hebraeum* followed by *Rhipicephalus glabroscutatum* were the most abundant. The animals on the farm were infested with 9 tick species of which *R. glabroscutatum* followed by *Haemaphysalis silacea* were the most abundant. The kudus were infested with 3 lice and 1 louse fly species.

Seasonal abundance

The seasonal abundances of *A. hebraeum, A. marmoreum, H. silacea, R. appendiculatus, R. evertsi evertsi, R. glabroscutatum* and a *Rhipicephalus* sp. (near *R. oculatus*) on only those kudus which were shot from February 1985 to January 1986 in the reserve, are graphically represented in Fig. 2.

The largest numbers of larvae of *A. hebraeum* were present from March to May and during July 1985, nymphs during March, November and December and adults during December. Peak numbers of larvae of *A. marmoreum* were present during February, April and May 1985. The larvae of *H. silacea* reached peak numbers from February to August and during December 1985 and January 1986, the nymphs from May to August 1985 and the adults during August and October 1985. The larvae of *R. appendiculatus* reached the largest numbers from March to June, the nymphs from June to October and the adults from February to April 1985 and during January 1986. The immature stages of *R. evertsi evertsi* were at their lowest from August to November. Large numbers of immature *R. glabroscutatum,* a 2-host tick, were present from March to

TABLE 4 Arthropod parasites of 9 kudus on the farm "Bucklands", eastern Cape Province

Arthropod species	Total number recovered					No. of kudus infested
Ixodid ticks	Larvae	Nymphs	Males	Females	Total	
Amblyomma hebraeum	157	24	14	4	199	7
Amblyomma marmoreum	54	2	0	0	56	5
Boophilus decoloratus	43	34	21	4	102	3
Haemaphysalis silacea	1 994	783	410	112(16)	3 299	9
Hyalomma marginatum rufipes	0	0	2	0	2	1
Rhipicephalus appendiculatus	1 638	796	70	20	2 524	9
Rhipicephalus evertsi evertsi	92	130	20	1	243	8
Rhipicephalus glabroscutatum	11 460	5 980	580	236(16)	18 256	9
Rhipicephalus sp. (near *R. oculatus*)	0	0	30	13	43	6
Lice	Nymphs		Adults		Total	
Damalinia sp.	16		0		16	1
Haematopinus taurotragi	30		22		52	1
Linognathus taurotragus	1 344		525		1 869	9
Louse flies	Adults				Total	
Lipoptena paradoxa	68				68	7

( ) = Number of maturing females, i.e. idiosoma of *H. silacea* >5,0 mm; *R. glabroscutatum* >4,0 mm in length. Females of the other tick species had not started to mature

TABLE 5 The mean numbers of ticks recovered from kudus examined during the same months in the Andries Vosloo Kudu Reserve and on the farm "Bucklands"

Ixodid tick species	Mean numbers of ticks recovered					
	Kudus in Kudu Reserve			Kudus on "Bucklands"		
	Larvae	Nymphs	Adults	Larvae	Nymphs	Adults
Amblyomma hebraeum	3 188	325	66	17	3	2
Amblyomma marmoreum	119	0	0	6	0,2	0
Boophilus decoloratus	0	0	3	5	4	3
Haemaphysalis silacea	505	81	70	222	87	58
Hyalomma marginatum rufipes	0	0	0	0	0	0,2
Hyalomma truncatum	0	0	0,3	0	0	0
Ixodes pilosus	0	0	0,3	0	0	0
Rhipicephalus appendiculatus	489	63	20	182	88	10
Rhipicephalus evertsi evertsi	21	11	1	10	14	2
Rhipicephalus glabroscutatum	873	376	113	1 273	664	91
Rhipicephalus sp. (near *R. oculatus*)	0	0	8	0	0	5
Rhipicephalus simus	0	0	0,5	0	0	0

August and adults during February and from September to December 1985. The adults of the *Rhipicephalus* sp. (near *R. oculatus*) were present in all months except May and June.

The 9 kudus shot at 3-monthly intervals (2 during June 1985) on the farm "Bucklands" could be paired with 8 animals shot during the same months in the adjacent AVKR. The burdens of these animals are compared in Table 5.

With the exeption of the larvae, nymphs and males of *A. behraeum,* for which the differences were significant, such differences between the farm and the reserve were not evident for any of the other tick species.

Addo Elephant National Park

Study site

The park is located in the eastern Cape Province at 33 ° 30 ′ S; 25 ° 45′ E and the vegetation is described as Valley Bushveld (Acocks, 1988).

Survey animals

Two adult male kudus were shot in this reserve during April 1985.

Arthropod burdens

The kudus were infested with 6 ixodid tick species, 1 louse and 1 louse fly species (Table 6).

More than 90 % of the tick population on the kudus consisted of *A. hebraeum.*

DISCUSSION

General observations

Utech, Seifert & Wharton (1978) and Sutherst, Wharton, Cook, Sutherland & Bourne (1979) found that the calves of domestic cattle carried fewer *Boophilus microplus* than their dams. Although the kudu calves were not necessarily the offspring of the kudu females shot during the same months in the Kruger National Park, comparisons of the calves' tick burdens with those of the females were nevertheless made. It was possible to pair 16 calves aged

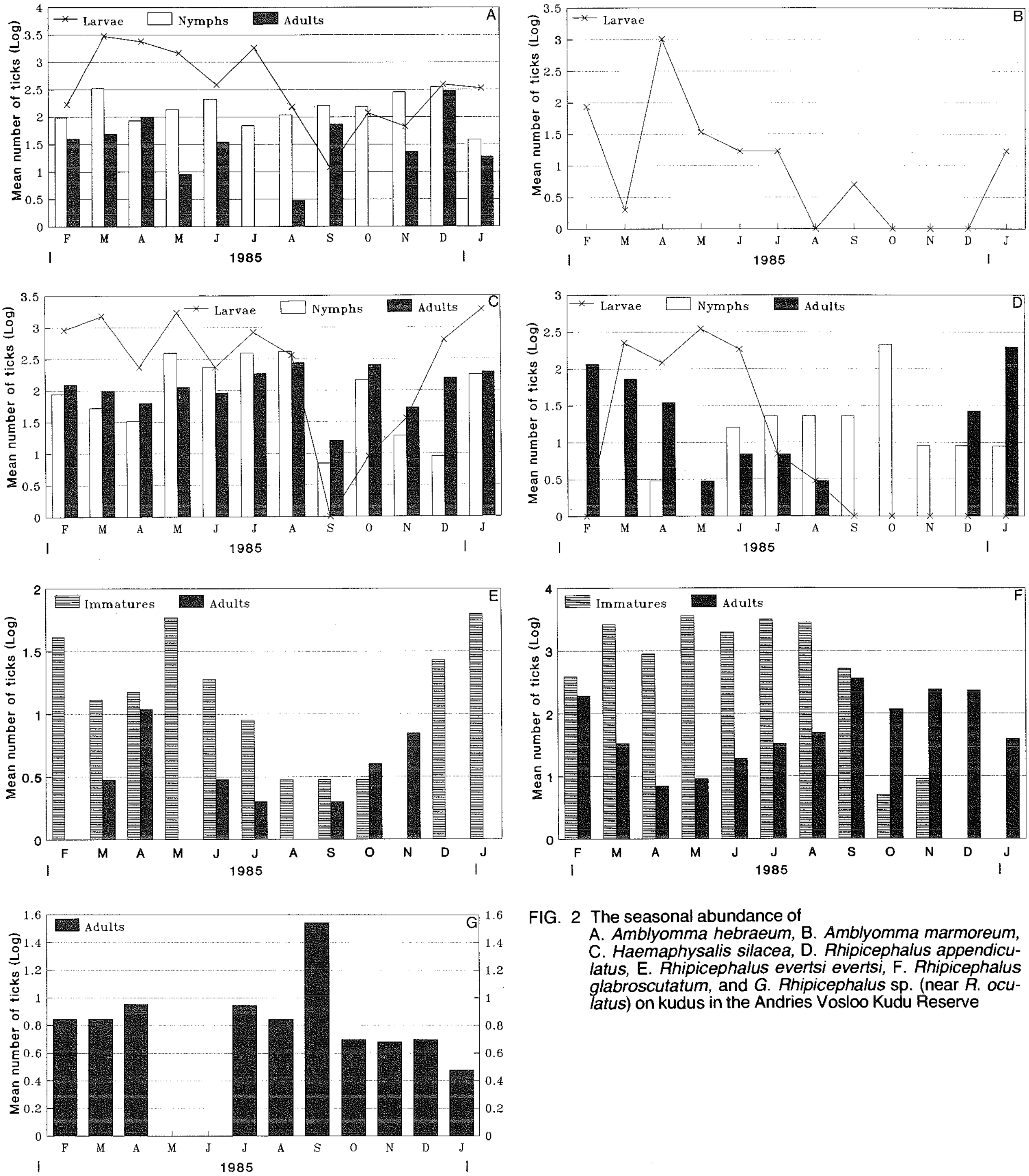

FIG. 2 The seasonal abundance of A. *Amblyomma hebraeum,* B. *Amblyomma marmoreum,* C. *Haemaphysalis silacea,* D. *Rhipicephalus appendiculatus,* E. *Rhipicephalus evertsi evertsi,* F. *Rhipicephalus glabroscutatum,* and G. *Rhipicephalus* sp. (near *R. oculatus*) on kudus in the Andries Vosloo Kudu Reserve

6 months or less with 16 adult females shot during the same months. No significant differences between the tick burdens of the calves and those of the cows were recorded. In fact, if one considers the size of the young calves compared with that of the cows, it would seem as if they are more prone to infestation than the cows.

Seifert (1971) recorded considerably more *B. microplus* on bulls than on domestic cows. He suggested that this strongly implies an influence of sex hormones on resistance. Our findings in the KNP show that adult male kudus carry significantly more nymphs (P=0,05), and males and females (P=0,001) of *A. hebraeum* and males and females (P=0,05) of *B. decoloratus* than do adult female animals. No such differences were recorded for any of the other tick species.

Horak, MacIvor, Petney & De Vos (1987) have suggested that the larger the host animal species the more likely it is to carry greater numbers of adult

TABLE 6 Arthropod parasites of 2 kudus in the Addo Elephant National Park

Arthropod species	Total number recovered					No. of kudus infested
Ixodid ticks	Larvae	Nymphs	Males	Females	Total	
Amblyomma hebraeum	14 957	1 165	30	10	16 162	2
Amblyomma marmoreum	17	0	0	0	17	2
Haemaphysalis silacea	985	125	119	44(4)	1 273	2
Hyalomma truncatum	0	0	1	0	1	1
Rhipicephalus evertsi evertsi	213	138	7	3	361	2
Rhipicephalus glabroscutatum	2	32	0	0	34	1
Lice	Nymphs		Adults		Total	
Linognathus taurotragus	22		6		28	1
Louse flies	Adults				Total	
Lipoptena paradoxa	11				11	2

( ) = Number of maturing females, i.e. idiosoma of *H. silacea* >5,0 mm in length. Females of the other tick species had not started to mature

A. hebraeum. The larger size of male kudus when compared to females may thus partially be responsible for the greater number of adult *A. hebraeum* carried by the former animals.

Kudus are good hosts of the immature stages of a large number of tick species (Horak & Knight, 1986; Tables 1 and 3). They are also good hosts of the adults of some species, such as *B. decoloratus, H. silacea, R. appendiculatus, R. glabroscutatum, R. zambeziensis* and a *Rhipicephalus* sp. (near *R. oculatus*). In addition adult male kudus must be considered good hosts of adult *A. hebraeum*.

Acaricidal treatment of the domestic livestock on "Bucklands" significantly affected the burdens only of *A. hebraeum* of kudus on the farm. This was probably due to the fact that cattle on the farm, which would have been good hosts for the adults of *A. hebraeum* as well as the other species, and the sheep and goats, which, with the exception of *R. glabroscutatum*, are generally poor hosts of the adults of most species, were all regularly treated with an acaricide and hence were poor hosts of all species. Thus, only the kudus, which, with the possible exception of the males, are not good hosts of adult *A. hebraeum*, but are good hosts of the adults of the other tick species, would have been largely responsible for maintaining the population of *A. hebraeum* on the farm. Petney & Horak (1987) state that the kudus clearly maintain a small but seemingly stable population of *A. hebraeum* on "Bucklands".

The eland and buffaloes on the reserve are very good hosts of adult *A. hebraeum* and individual animals may harbour more than 1 000 adult ticks (Horak, MacIvor, Petney & De Vos, 1987). They are also good hosts of the adults of the other tick species. These animals would largely be responsible for the large total burdens of *A. hebraeum* on the kudus on the reserve and they and the kudus themselves for the total burdens of the other tick species on the kudus.

The role kudus may play as reservoir hosts of ticks infesting cattle in mixed cattle and game ranching operations will depend on the population density of the former animals. As kudus are browsers (Owen-Smith, 1979; Novellie, 1983) their densities will be dependent upon the amount and quality of available browse. Thus in the Valley Bushveld of the eastern Cape Province where browse, particularly the spekboom *(Portulacaria afra)* is abundant, kudu density can be considerably higher than in the north-eastern Transvaal. Conventional stock fences do not serve as a barrier to kudus and consequently they could also disseminate ticks over considerable distances and several farms.

Both the tick reservoir status of kudus and their mobility could be advantageous to the stock farmer in that they could serve as a source of infected ticks on a cattle farm. This would help maintain immunity to diseases such as babesiosis *(Babesia bigemina)* and heartwater *(Cowdria ruminantium)* in cattle otherwise kept relatively tick-free by regular acaricidal treatment.

Amblyomma hebraeum

The 28 adult male kudus examined in the KNP harboured a mean of 1 003 larvae, 131 nymphs, 16 males and 8 females of this tick compared with 2 001, 223, 29 and 16, respectively, for the 16 males examined in the AVKR. The latter burdens were almost exactly double the former for each life stage as well as for the total. The larval:nymphal:adult ratio was virtually identical for male kudus on the 2 reserves being approximately 44:5:1.

This tick was introduced into the eastern Cape Province during the 1830's, probably on cattle from Zululand (Theiler, 1975; Provost & Bezuidenhout, 1987). The large numbers recovered from the kudus in this region confirm that it has become well established there. The fact that the kudus in the AVKR harboured nearly twice the burdens of those in the KNP does not, however, imply that the former habitat is more favourable than the latter; it is more a reflection of stocking density. The KNP is close to 2 M ha in extent and contains approximately 15 000 kudus, 400 eland, 30 000 buffaloes and 8 000 giraffes (all good hosts of adult *A. hebraeum*) resulting in an approximate stocking density of 1 of these animals per 37 ha. In the Kudu Reserve the approximate stocking density for kudus, eland and buffaloes combined is 1 animal per 9,4 ha.

The immature stages of *A. hebraeum* have a wide host range (Theiler, 1962; Norval, 1974a). They utilize not only the same hosts as the adults, but a variety of small domestic and wild ruminants as well as scrub hares and helmeted guineafowls (Horak, MacIvor, Petney & De Vos, 1987). The higher stocking density in the AVKR is also reflected in the tick burdens of those hosts that harbour only immature stages; scrub hares had mean burdens of 46 larvae and 15 nymphs (Horak & Fourie, 1991) compared with 11 larvae and 11 nymphs on scrub hares in the KNP (Horak, Spickett & Braack, unpublished data). Helmeted guineafowls in the AVKR harboured 568 larvae and 26 nymphs, and those in the KNP 185 and 17 (Horak, Spickett, Braack & Williams, 1991). The hares, kudus and guineafowls in the AVKR were all examined at the same time, whereas in the KNP the hares and guineafowls were examined several years after the kudus.

If the number of immature ticks carried by female kudus and the smaller antelope as well as those harboured by scrub hares and guineafowls are taken into account the ratio of parasitic larvae and nymphs to adults will shift even further in favour of the immature stages.

The largest burden of adult ticks harboured by a single kudu was 72 males and 58 females recovered from a male shot in the KNP during January 1982 and 185 males and 119 females from a male shot in the AVKR during December 1985. The tick burdens of the 2 kudus examined in the Addo Elephant National Park indicate that burdens of *A. hebraeum* could possibly be even higher on kudus in this reserve than in either of the other reserves.

Despite only 1 animal being examined each month in the AVKR, larvae appeared to be more abundant during late summer and winter, nymphs during early summer and again in late summer and adults from early to late summer. This pattern of seasonal abundance corresponds to that observed by Knight & Rechav (1978) on kudus and by Rechav (1982) on cattle examined in the same locality, and is probably regulated by climate. In the KNP, where temperatures are higher than those in the eastern Cape Province, no clear pattern of seasonal abundance was evident and the tick's life cycle appeared to continue uninterrupted throughout the year.

Amblyomma marmoreum

Tortoises are the preferred hosts for all parasitic stages of this tick (Theiler, 1962; Norval, 1975b; Dower, Petney & Horak, 1988). Helmeted guineafowls, scrub hares, caracal, kudus, eland and cattle are all good hosts of the larvae if the numbers recovered and percentage of hosts infested are taken into account (Horak, MacIvor, Petney & De Vos, 1987; Horak & Fourie, 1991). With the possible exception of guineafowls, none of these animals are good hosts of the nymphs.

The large total number of larvae recovered from the kudus in the AVKR compared with those on "Bucklands" and in the KNP is due to 2 animals. One of these harboured 1 008 and the other 865 larvae.

The period of peak larval abundance (January to July) on kudus in the AVKR was longer than that on animals in the KNP (April to June). The seasonal abundance of larvae on helmeted guineafowls in the AVKR was similar to that on the kudus at the same locality, while that on guineafowls in the KNP extended from February or March to July or August (Horak, Spickett, Braack & Williams, 1991). The only nymphs recovered were from a kudu examined on "Bucklands" during December 1986.

Boophilus decoloratus

This was by far the most abundant tick on the kudus in the KNP, a finding also applicable to blue wildebeest and Burchell's zebras examined in this park (Horak, De Vos & Brown, 1983; Horak *et al.*, 1984). Drag-sampling of 32 of the 35 vegetation zones in the KNP during March 1988 indicated that *A. hebraeum* was the dominant species (Spickett, Horak, Braack & Van Ark, 1991), but this may well have been due to the month in which the samples were collected. Monthly drag-sampling of 2 vegetation zones near the study site over a period of 3 years, from 1988 to 1991, indicated that *R. zambeziensis* followed by *B. decoloratus* were most abundant in the zone north of the study site and *A. hebraeum* followed by *R. appendiculatus* and then *B. decoloratus* in the zone east of the study site (Horak, Spickett & Braack, unpublished data). Although it is possible that *B. decoloratus* was the dominant tick on the vegetation within the study area this seems unlikely in the light of the drag-sampling data from the 2 zones.

Two possible reasons for the large numbers of *B. decoloratus* on the kudus are, firstly that this is a 1-host tick, spending approximately 21 days on an animal in order to complete its parasitic life cycle (Londt & Spickett, 1976). Thus *B. decoloratus* recovered at slaughter represent ticks acquired during the previous 3 weeks compared with the multi-host tick species in which each stage, with the possible exception of males, spends approximately only 7 days on the host. Secondly the loss between the developmental stages, which do not each have to seek a new host in the case of a 1-host tick, is considerably less than that encountered with multi-host ticks. Furthermore kudus must be accepted as one of the preferred hosts of *B. decoloratus*. In the present study they harboured mean total burdens of 3 407 ticks of this species compared with 548 on blue wildebeest and 1 827 on Burchell's zebras examined in the KNP during earlier studies (Horak, De Vos & Brown, 1983; Horak *et al.*, 1984).

The overall ratio of larvae to nymphs to adults is 3,0:2,0:1,0 and this implies a good translation to adulthood without too much loss during the developmental stages and further confirms that kudus are one of the preferred hosts of *B. decoloratus*. On blue wildebeest and Burchell's zebras examined in the KNP during earlier studies these ratios were 8,9:1,7:1,0 and 3,0:1,1:1,0 respectively, indicating that wildebeest are poor hosts and zebras good hosts (Horak, De Vos & Brown, 1983; Horak *et al.*, 1984).

The ratios of males to females on the 3 host species were 1,98:1,00; 1,35:1,00 and 2,07:1,00 for the kudus, wildebeest and zebras, respectively. The most logical explanations for this disparity seem to be firstly, that because of the larger size of the females they are more easily rubbed or groomed off by the host and secondly, that the males remain attached for longer than the females. This differs markedly from the findings of Davey & Cooksey (1988) for *B. microplus* and *Boophilus annulatus* on artificially infested cattle. They recovered fewer males than females and recorded ratios of 1,00:1,36 and 1,00:1,35 males to females for the 2 tick species. They ascribed these differences to a selective mortality of males at some point in their development resulting in more females reaching the adult stage.

If one accepts that the kudus in the KNP acquired infestation on a daily basis and that female *B. decoloratus* spend 6 days on the animals, of which the last day is spent engorging before detaching (Londt & Spickett, 1976), then approximately 1/6 of all females should be engorging. This would imply that there should have been a total of 3 023 engorging females compared with the 360 actually recovered. This small number could be due to acquired resistance in the kudus as noted in the case of *Bos indicus* cross breeds of cattle and *B. microplus* (Sutherst, Maywald, Bourne, Sutherland & Stegeman, 1988). In cattle this resistance is only fully evident at approximately 2 years of age, but was already effective in the kudu calves. The small number could also be due to the fact that the kudus were usually shot after 08:00 h whereas many of the engorged females may have detached earlier.

It is probable that red-billed oxpeckers, which are commonly found on kudus in the KNP, also played a role in reducing the numbers of engorging female *B. decoloratus*. This tick is one of the preferred foods of these birds (Bezuidenhout & Stutterheim, 1980). Blue wildebeest and Burchell's zebras examined in the KNP also harboured small numbers of engorging female *B. decoloratus* compared to the total burdens of ticks of this species (Horak, De Vos & Brown, 1983; Horak *et al.*, 1984).

The peaks of abundance recorded for *B. decoloratus* on the kudus during September and October 1981 and November and December 1982 correspond to the peaks recorded during October 1978 on blue wildebeest and September 1979 and 1980 and December 1980 on Burchell's zebras in the KNP. These peaks, which occurred in spring or early summer, could be due to synchronous hatching of large numbers of larvae from eggs that had overwintered (Robertson, 1981; Spickett & Heyne, 1990). The spring rise could also possibly be coupled to a decrease in host resistance resulting from poor nutrition during the preceding winter and early spring months (Sutherst *et al.*, 1979).

Baker & Ducasse (1967) recovered peak numbers of *B. decoloratus* from calves in Natal from November to June. With the exception of 1 year when large numbers of ticks were present during November and December, Robertson (1981) recovered most *B. decoloratus* from cattle on a coastal property in the eastern Cape Province from February to June during a 4 year survey. Spickett, De Klerk, Enslin & Scholtz (1989) recorded peaks in the activity of *B. decoloratus* on cattle in the south-eastern Transvaal during February, July, October and December. In Natal Baker, Ducasse, Sutherst & Maywald (1989) recorded peak activity on cattle during spring and autumn. Rechav & Kostrzewski (1991) found peaks of activity in March/April, July, September/October, and December/January on cattle in the northern Transvaal. Horak, Williams & Van Schalkwyk (1991) recovered most *B. decoloratus* from Merino sheep during July and November in the eastern Orange Free State and in the eastern Cape Province. It would thus appear that in South Africa *B. decoloratus* may be encountered in peak numbers during any or all seasons. Nevertheless, spring and late summer seem to be the most preferred times.

The inland Valley Bushveld regions of the eastern Cape Province are not a suitable habitat for the free-living stages of *B. decoloratus*. Very few were recovered from the kudus in the AVKR and on "Bucklands" and none on the kudus from the Addo Park. Knight & Rechav (1978) also recovered only a few *B. decoloratus* from the kudus they examined on "Bucklands" and its environs.

In the KNP 21,3 % of all *B. decoloratus* were attached to the lower legs and feet of the kudus, 13,9 % to the heads and ears, 63,4 % to the necks, bodies and upper legs and 1,4 % to the tails. Only 10,9 % of the population of female ticks was attached to the legs and lower feet compared with 24,9 % of the males, indicating a selective loss of the larger female life stage from this attachment site.

Furthermore only 4,4 % of all engorging females were recovered from the lower legs and feet while 81,1 % and 6,1 % were recovered from the necks, bodies and upper legs and from the tails, respectively. This indicates that the lower legs and feet were particularly unfavourable for the completion of the female life cycle whereas the tails seemed to afford most protection for these large ticks. On Burchell's zebras examined in the park at an earlier occasion 8,0 % of *B. decoloratus* were attached to the lower legs and feet, 8,9 % to the heads and ears and 83,1 % to the necks, bodies, upper, legs and tails (Horak *et al.*, 1984).

Haemaphysalis silacea

According to Howell, Walker & Nevill (1978) this tick is found in well-wooded ravines and river valleys in the eastern Cape Province and in Natal. Hence its presence on kudus in the Valley Bushveld vegetation of the AVKR, "Bucklands" and Addo Elephant National Park. It has a wide host range including kudus, eland, sheep, goats, cattle and helmeted guineafowls (Knight & Rechav, 1978; Horak, Potgieter, Walker, De Vos & Boomker, 1983; Horak & Knight, 1986).

In the present survey 27,8 % of all males and 59,5 % of all females were found attached on the tails of the kudus in the AVKR. In addition 84,8 % of all the engorging female ticks were recovered from the tails. This need not necessarily imply that the tail is a preferred site of attachment for female ticks of this species, but rather that the long hair on the tail affords greater protection against grooming for this larger life stage and particularly for those that are engorging.

As only 1 kudu was examined at each occasion the pattern of seasonal abundance on these animals is not reliable. It would, however, appear as if the life cycle continues throughout the year. Combining the findings of this study with those of Norval (1975a), Knight & Rechav (1978), Rechav (1982) and Horak, Williams & Van Schalkwyk (1991), larvae are most numerous from summer to early winter, nymphs from autumn to spring and adults in spring and in late summer.

Hyalomma spp.

The distribution of *Hyalomma marginatum rufipes* includes the Valley Bushveld regions of the eastern Cape Province, while that of *Hyalomma truncatum* includes the latter region as well as the KNP (Howell *et al*., 1978). Scrub hares are the preferred hosts of the immature stages of both these ticks (Horak & MacIvor, 1987; Rechav, Zeederberg & Zeller, 1987; Horak & Fourie, 1991). Using the number of ticks recovered from scrub hares as criterion the Valley Bushveld is not a good habitat for the 2 *Hyalomma* spp. (Horak & MacIvor, 1987; Horak & Fourie, 1991), whereas the KNP is a good habitat for *H. truncatum* (Horak, Spickett & Braack, unpublished data). The small number of adult ticks recovered from the kudus in the KNP is therefore evidence that these animals are not good hosts of this tick. The preferred hosts of the adults are eland and zebras and probably giraffes (Rechav *et al*., 1987; Horak, Fourie, Novellie & Williams, 1991). The small numbers of the 2 *Hyalomma* spp. on the kudus in the eastern Cape Province are a reflection both of the unsuitability of the habitat and the host species.

Adult *H. truncatum* were generally recovered from the kudus in the KNP during any month from January to July. In the AVKR and on "Bucklands" *Hyalomma* spp. were recovered in March, April and during June.

Ixodes pilosus

In the Cape Province this tick is generally confined to the Sourveld coastal regions (Howell *et al*., 1978). Its presence on the animals in the AVKR probably reflects its most northern distribution at this particular point. The preponderance of parasitic females over males is typical for this species (Norval, 1974b; Horak, Sheppey, Knight & Beuthin, 1986), in which mating probably takes place off the host.

Rhipicephalus appendiculatus

The KNP, AVKR and "Bucklands" all lie within the geographic distribution of this tick as described by Howell *et al.* (1978). The Addo Elephant National Park is situated to the west of the southern limits of this distribution and no *R. appendiculatus* were recovered from the kudus examined in this park.

The adults appear to prefer large bovids such as cattle, eland and buffaloes but kudus, sable antelopes and impala are also good hosts (Norval, Walker & Colborne, 1982; Horak, Potgieter, Walker, De Vos & Boomker, 1983). The immature stages can also be recovered in large numbers from these hosts, but may be encountered in similar large numbers on Burchell's zebras and on a variety of smaller animals such as sheep, goats, small antelope and scrub hares (Norval *et al*., 1982; Horak *et al*., 1984; Horak & Knight, 1986).

The taxonomic differences between *R. appendiculatus* and *R. zambeziensis* have only fairly recently been described (Walker, Norval & Corwin, 1981). We have always been able to distinguish between the nymphs of the 2 species and did so for each of the separate skin regions examined. The larvae and adults, however, were only differentiated once the ticks for each kudu had been pooled and hence no preferred sites of attachment for these stages can be identified. In the KNP 21,8 % of nymphs of *R. appendiculatus* were recovered from the lower legs and feet, 53,1 % from the heads and ears and 25,1 % from the necks, upper legs, bodies and tails of the kudus. These figures were 27,4 %, 50,1 % and 22,5 % respectively for the animals in the AVKR. Baker & Ducasse (1967) recovered 58,0 % of nymphs from the heads and ears of live-sampled cattle in Natal and 16,6 % from their legs and feet. In Uganda Kaiser, Sutherst & Bourne (1982) recovered 24 % of nymphs from the head and ears of live-sampled cattle and 20 % from around the hooves.

The overall ratio of larvae to nymphs to adults of 2,49:0,67:1,00 on kudus in the KNP and 8,54:1,51:1,00 in the AVKR compared with the 16:4:1 we consider closer to the normal population distribution for a 3-host tick, can have various explanations. Firstly, the recovery of the immature stages by the scrubbing method employed may not be as effective as for the larger adults. Secondly, smaller antelope species and scrub hares may carry substantial numbers of immatures with few or no adults (Horak, 1982; Boomker, Du Plessis & Boomker, 1983; Horak & Knight, 1986). Large numbers of *Rhipicephalus* spp. nymphs and probably also larvae, may selectively be removed by oxpeckers (Bezuidenhout & Stutterheim, 1980). Baker & Ducasse (1967) recorded ratios of 4,10 larvae to 2,87 nymphs to 1,00 adults on live-sampled cattle in Natal.

The ratio of males to females of 1,78:1,00 on kudus in the KNP and 1,86:1,00 in the AVKR compares favourably with that of 1,84:1,00 and 1,88:1,00 recorded by Londt, Horak & De Villiers (1979) and Horak (1982) on cattle in the northern Transvaal and of 1,99:1,00 found by Kaiser *et al.* (1982) on cattle in Uganda. The latter authors recorded a ratio of 1,84:1,00 only 7 days after the hosts had been picked clean of ticks and suggested that further experiments to explain this phenomenon were necessary. Bezuidenhout & Stutterheim (1980) found that oxpeckers consume nearly twice as many female *Rhipicephalus* spp. as they do males.

If one assumes that female *R. appendiculatus* spend approximately 7 days on their hosts

(Minshull, 1982), that these hosts are constantly exposed to infestation during periods of peak seasonal abundance of the ticks, and that the female ticks engorge during the last 24 h of their attachment, then approximately 1/7 (14,3 %) of the female ticks should be maturing. On the kudus in the KNP only 1,8 % were maturing, whereas this figure was 13,3 % for the animals in the AVKR. Minshull (1982) found that most engorged females of *R. appendiculatus* detached from artificially infested cattle between 06:00 and 08:00 h. As most of the kudus in the KNP were shot after 08:00 h many engorged female ticks could already have detached. The same argument does not apply to the animals in the AVKR, which were also shot after 08:00 h and yet harboured a large proportion of maturing females. Oxpeckers, which as mentioned previously, prefer female *Rhipicephalus* spp. ticks to males, may also be responsible for the small number of maturing ticks in the KNP. These birds were not present in the AVKR.

The seasonal abundance of the adults and nymphs in the 2 reserves was reasonably similar. In the AVKR increased numbers of larvae were recovered 1 month earlier than in the KNP, whereas peak larval activity extended for 1 month longer in the latter reserve. In general terms larvae were active from late summer to winter or spring, nymphs from winter to spring and adults from mid-summer to autumn. This pattern of abundance corresponds to that observed on cattle in Natal by Baker & Ducasse (1967), in the northern Transvaal by Horak (1982) and in the eastern Cape Province by Rechav (1982).

Short & Norval (1981) state that the pattern of seasonal abundance is chiefly dependent on the activity period of the adults and that this is regulated by the combined influences of humidity, temperature and daylength. Unfortunately too few animals were examined in each of the reserves to determine accurately the periods of activity of the adults. If, however, tick counts from cattle slaughtered at monthly intervals over a 2 year period on "Bucklands" at the same time as the kudus in the AVKR (Horak, unpublished data), are added to the latter data it would appear as if peak adult activity extends from December to February in this region of the eastern Cape Province. This corresponds exactly with that recorded by Rechav (1981) in this area. Taking the mean values for the 2 year study in the KNP into account peak adult activity occurred from February to May in this park.

Rhipicephalus evertsi evertsi

Although this tick has a very widespread distribution in South Africa (Howell *et al.*, 1978), it never occurs in very large numbers except on zebras and eland (Horak *et al.*, 1984; Horak, Fourie, Novellie & Williams, 1991). If the burdens of the kudus in the KNP are compared with those of Burchell's zebras examined a few years previously in the same park (Horak *et al.*, 1984) it is obvious that kudus are not a preferred host of *R. evertsi evertsi*. The mean burdens of the zebras comprised 606 larvae, 259 nymphs and 76 adults compared with 95 larvae, 10 nymphs and 2 adults on the kudus. In addition, it would appear as if kudus do not, or cannot, harbour many nymphs of this 2-host tick, of which the immature stages occur in the ear canal. This could affect the successful translation of larvae to nymphs when many larvae are present. In the KNP mean burdens of 95 larvae translated into only 10 nymphs compared with mean burdens of 16 larvae on kudus in the AVKR and "Bucklands" combined, translating into 11 nymphs. The largest number of nymphs recovered from a kudu was 72, compared with 626 from an eland and 1 944 from a zebra (Horak, unpublished data).

Combining the total numbers of adult *R. evertsi evertsi* recovered from all the kudus examined in the present surveys, the ratio of males to females is 2,75:1,00. The marked preponderence of males is probably because more males than females may be recovered from animals even within 1 week of them having been picked clean of ticks, and that males may remain on the host for longer than females and thus their numbers accumulate (Kaiser *et al.*, 1982).

No clear pattern of seasonal abundance was evident. The fact that both adults and immatures may be present throughout the year indicates that more than 1 life cycle can be completed annually and that development is continuous in the regions in which the present surveys were conducted. This corresponds to the observations made by Matson & Norval (1977) on cattle in Zimbabwe, Horak, Williams & Van Schalkwyk (1991) on sheep in the Orange Free State and in the eastern Cape Province, Horak *et al.* (1984) and Horak, Fourie, Novellie & Williams (1991) on Burchell's zebras in the KNP as well as on Cape mountain zebras and eland in the Karoo respectively.

Rhipicephalus glabroscutatum

The geographic distribution of this tick has been described by MacIvor (1985). It is largely confined to the eastern Cape Province where it inhabits non-coastal areas of low rainfall characterized by Karoo and Karoid vegetation, with isolated pockets extending into the western Cape Province. Its original hosts were probably the antelope inhabiting these regions and more particularly eland, kudus, mountain reedbuck and common duikers (MacIvor, 1985; Horak & Knight, 1986; MacIvor & Horak, 1987; Horak, Fourie, Novellie & Williams, 1991) and probably also bushbuck. Scrub hares may harbour the immature stages only (Horak & Knight, 1986; Horak & Fourie, 1991). With the introduction of domestic stock into these regions *R. glabroscutatum* now also infests goats, sheep and cattle (MacIvor & Horak, 1984, 1987; MacIvor, 1985; Horak & Knight, 1986; Horak, Williams & Van Schalkwyk, 1991).

According to MacIvor (1985) the preferred site of attachment is the legs and feet. In the present survey 83,9 % of all immature ticks and 95,7 % of all adults were recovered from the lower legs and feet of the kudus in the AVKR and on "Bucklands". MacIvor & Horak (1987) state that while goats may frequently harbour large numbers of adult ticks between their hooves none where found between the hooves of the antelope they examined on one of the farms on which they worked. They suggested that this difference might be due to the structure of the hooves with the concave axial corium of the goat hoof resulting in a space in the interdigital region which could be exploited by ticks, while the straight axial corium of the antelopes' hooves limited this space.

The seasonal abundance of *R. glabroscutatum* on a variety of host species has been determined in the eastern Cape Province (Knight & Rechav, 1978; MacIvor & Horak, 1984, 1987; Horak, Williams & Van Schalkwyk, 1991; Horak, Knight & Williams, 1991; Horak & Fourie, 1991), the Karoo (Horak, Fourie, Novellie & Williams, 1991) and the south-western Cape Province (Horak, Sheppey, Knight & Beuthin, 1986). In all these regions the greatest numbers of immature ticks were recovered from March to August and of adults from September to January or February. It is probable that only 1 generation is completed annually (MacIvor, 1985).

Rhipicephalus sp. (near *R. oculatus*)

The taxonomic problems that exist between this tick and *Rhipicephalus oculatus* have been discussed by Walker (1991). Its geographic distribution has also been briefly addressed by Walker (1991). It is fairly common in certain Valley Bushveld regions of the eastern Cape Province, where the adults may be found on scrub hares, kudus, cattle, sheep and goats (Horak & Knight, 1986).

In the present study 10,6 % of the ticks were recovered from the heads and ears of the kudus, 80,8 % from the necks, bodies and upper legs, and equal proportions from the lower legs plus feet and from the tails. May and June appear to be the only months in which no adult ticks are present. This pattern of seasonal abundance was confirmed on scrub hares, sheep, goats and cattle examined in the AVKR or on "Bucklands" at the same time as the kudus (Horak, unpublished data).

Rhipicephalus simus

Although this tick has a widespread distribution, mainly in the eastern regions of South Africa (Howell *et al.*, 1978), it is seldom encountered in large numbers. The preferred hosts of the adults are large monogastric animals such as zebras, warthogs, large wild carnivores and dogs, but they also occur on cattle (Howell *et al.*, 1978; Horak *et al.*, 1984; Horak, Jacot Guillarmod, Moolman & De Vos, 1987; Horak *et al.*, 1988).

In the KNP a total of 15 adults were recovered from the 95 kudus examined, while 33 Burchell's zebras, 7 large carnivores and 51 warthogs examined in the park harboured totals of 381, 669 and 560 adults respectively (Horak *et al.*, 1984; Horak Jacot Guillarmod, Moolman & De Vos, 1987; Horak *et al.*, 1988). The 25 kudus shot in the AVKR and on "Bucklands" harboured a total of only 6 adults while 46 cattle examined on "Bucklands" at the same time harboured 48 adults (Horak, unpublished data). It is thus obvious that kudus are not good hosts of adult *R. simus*. The immature stages prefer rodents (Norval & Mason, 1981).

Twelve of the 15 ticks recovered from the kudus in the KNP and all 6 ticks from the kudus in the AVKR were collected from the lower legs and feet of the animals. Too few ticks were present to determine any pattern of seasonal abundance.

Rhipicephalus zambeziensis

This tick has only fairly recently been described and its morphology compared with that of *R. appendiculatus* (Walker *et al.*, 1981). Its ecology and that of *R. appendiculatus,* with particular emphasis on Zimbabwe, have also been described (Norval *et al.*, 1982). In South Africa *R. zambeziensis* has to date only been found in the Transvaal and more particularly on farms in the west of the province as well as in the northern and southern regions of the KNP in the east of the province (Norval *et al.*, 1982). This distribution falls entirely within that of *R. appendiculatus* as illustrated by Howell *et al.* (1978). However, more recent data from the KNP indicate that there are areas of overlap as well as regions in which one or the other tick occurs almost exclusively (Horak, Spickett & Braack, unpublished data). The study site from which the kudus in the KNP were collected lies within such a region of overlap. To the east and west of this site there are zones within the KNP in which *R. appendiculatus* occurs almost exclusively and to the north a zone in which *R. zambeziensis* occurs virtually exclusively (Horak, Spickett & Braack, unpublished data).

Although large carnivores, warthogs, bushpigs and equids can be infested, the preferred hosts of *R. zambeziensis* seem to be impala, bushbuck, nyalas, kudus, eland and probably cattle and buffaloes (Norval *et al.*, 1982; Walker, 1991). In the present study 91 of the 95 kudus were infested. Two of the 4 kudus that were not infested were examined during November and 1 during December, both months of generally low abundance for all stages of development (Fig. 1). The total numbers of *R. appendiculatus* and *R. zambeziensis* recovered from the kudus suggest that the zone in which they were examined is equally favourable for both tick species.

As mentioned earlier for *R. appendiculatus*, we can unfortunately also only give the preferred sites of attachment for the nymphal stage of *R. zambeziensis.* Of these 81,4 % were attached to the lower legs and feet, 9,2 % to the head and ears, 8,6 % to the neck, body and upper legs and 0,8 % to the tail. Thus the nymphs of *R. appendiculatus* prefer the heads and ears and those of *R. zambeziensis* the lower legs and feet of kudus.

The ratio of larvae to nymphs to adults of 9,92:1,42:1,00 indicates that the kudus are good hosts of larvae, while many nymphs possibly fed on other host species. The total numbers of larvae of *R. appendiculatus* and *R. zambeziensis* recovered from the kudus were reasonably similar but fewer nymphs and adults of *R. zambeziensis* were recovered. This suggests that kudus may be less favoured as hosts of these stages than for those of *R. appendiculatus.*

The ratio of male to female *R. zambeziensis* of 1,99:1,00 is comparable to that of *R. appendiculatus* on the same animals. As in the case of the latter tick, few maturing females were recovered.

According to Norval *et al.* (1982) the seasonal abundances of these 2 ticks are similar in Zimbabwe. The present results confirm this finding and the periods of seasonal activity are almost identical; larvae exhibiting peak abundance in autumn and winter, nymphs during winter and spring and adults in late summer.

Lice

Damalinia sp. have not previously been recovered from kudus, while *Haematopinus taurotragi* and *Linognathus taurotragus,* which were both originally described from eland, have (Ledger, 1980). The lice infestations were always light and no pattern of seasonal abundance or host age-preference or host sex-preference could be determined.

Flies

The majority of kudus at each survey locality were infested with the louse fly *Lipoptena paradoxa.* The seasonal abundance of this fly on the kudus and other aspects of its biology will be reported separately.

Pentastomid nymphs

In earlier surveys Horak, De Vos & Brown (1983) and Horak *et al.* (1988) recovered the nymphs of *Linguatula nuttalli* from 12 (21,8 %) of 55 blue wildebeest and 18 (35,3 %) of 51 warthogs examined in the KNP. Kudus would appear to be more susceptible to infection as 60 (63,2 %) of the 95 animals examined in the park were infected. Lions are the final host of this parasite.

ACKNOWLEDGEMENTS

This study is part of the Wildlife Research Programme of the Faculty of Veterinary Science, University of Pretoria.

We wish to express our thanks to the National Parks Board of Trustees, who placed the kudus in the Kruger National Park and Addo Elephant National Park at our disposal. The Division of Nature Conservation of the Cape Provincial Administration and Mr W. A. Phillips made the animals in the Andries Vosloo Kudu Reserve and on the farm "Bucklands" respectively, available to us.

We are most appreciative of the assistance of Messrs B. D. de Klerk, C. Cheney, P. D. Burdett and M. M. Knight with the necropsies and Mesdames Gail Walter and Shelley Beuthin and Mr E. J. Williams with the parasite recoveries. Miss Andrea van Niekerk drew the graphs. Dr Jane Walker confirmed the identity of the *Rhipicephalus* sp. (near *R. oculatus*).

This research was funded by the National Parks Board, the Cape Provincial Administration, Pretoria University, the South African Nature Foundation, the Meat Board and the Council for Scientific and Industrial Research.

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Parasites of domestic and wild animals in South Africa. XXXIV. Arthropod parasites of nyalas in north-eastern KwaZulu-Natal

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ABSTRACT

HORAK, I.G., BOOMKER, J. & FLAMAND, J.R.B. 1995. Parasites of domestic and wild animals in South Africa. XXXIV. Arthropod parasites of nyalas in north-eastern KwaZulu-Natal. *Onderstepoort Journal of Veterinary Research,* 62:171–179

Seventy-three nyalas (*Tragelaphus angasii*) in the Umfolozi, Mkuzi and Ndumu Game Reserves in north-eastern KwaZulu-Natal were examined for arthropod parasites during 1983 and 1984. In addition, six animals were examined during 1994. Ten ixodid tick species, two louse species and a louse fly species were recovered. The nyalas were good hosts of all stages of development of *Boophilus decoloratus, Rhipicephalus appendiculatus* and *Rhipicephalus muehlensi* and the immature stages of *Amblyomma hebraeum* and *Rhipicephalus maculatus.*

Adult male animals harboured more adult ticks, biting lice and louse flies than did adult females.

B. decoloratus was generally most abundant from October to May. The larvae of *R. appendiculatus* peaked from April to October, nymphs from July to October and adults, on adult male nyalas, from February to May. Larvae of *R. maculatus* were most abundant from May to July and nymphs from June to October. The immature stages of *A. hebraeum* and all stages of *R. muehlensi* were present throughout the year.

Keywords: Arthropod parasites, nyalas, north-eastern KwaZulu-Natal, *Tragelaphus angasii*

INTRODUCTION

Several surveys of ixodid ticks infesting domestic and wild animals in KwaZulu-Natal, have already been conducted. Baker & Ducasse (1967) and Baker, Ducasse, Sutherst & Maywald (1989) examined cattle, and Baker & Ducasse (1968), goats. Buffaloes *(Syncerus caffer)*, nyalas *(Tragelaphus angasii)*, common reedbuck *(Redunca arundinum)*, impalas *(Aepyceros melampus)*, bushbuck *(Tragelaphus scriptus)*, common duikers *(Sylvicapra grimmia)*, red duikers *(Cephalophus natalensis)*, bushpigs *(Potamochoerus larvatus)* and scrub hares *(Lepus saxatilis)* were examined by Horak, Potgieter, Walker, De Vos & Boomker (1983), Horak, Keep, Flamand & Boomker (1988), Horak, Keep, Spickett & Boomker (1989), Horak, Boomker & Flamand (1991a) and Horak, Spickett, Braack, Penzhorn, Bagnall & Uys (1995). Baker & Keep (1970) published a checklist of ticks infesting the larger wild animals in KwaZulu-Natal game reserves, while Keep (1971) produced such a list specifically for nyalas.

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Accepted for publication 25 July 1995—Editor

Nyalas in the north-eastern KwaZulu-Natal game reserves had to be culled during the late 1970s and early 1980s because their numbers exceeded the carrying capacity of the land. Culling or relocation has subsequently continued at irregular intervals. In conjunction with this activity, parasites were collected from some of the culled animals and Boomker, Horak & Flamand (1991) reported on the helminths recovered. They also summarized the available data on the morphometrics, feeding and behaviour of nyalas and briefly described the physiography of the Umfolozi, Mkuzi and Ndumu Game Reserves.

According to Smithers (1983), male nyalas are considerably taller and heavier than females. Adult males are horned and slatey-grey to dark brown in colour with a few white, vertical stripes on the body. They have a dorsal crest of long hair from the back of the head to the base of the tail and a heavy fringe of long hair on the under-parts of the neck and along the middle line of the chest and belly. Females are hornless, bright chestnut in colour and have up to 18 white, vertical stripes on their bodies. Nyalas are predominantly browsers and have a restricted habitat in that they are usually found in thickets in dry savanna woodland or riverine woodland (Smithers 1983).

The present paper records the ectoparasite burdens of nyalas culled in the Umfolozi, Mkuzi and Ndumu Game Reserves in north-eastern KwaZulu-Natal.

MATERIALS AND METHODS

Study areas and animals

Umfolozi

The Umfolozi Game Reserve (28°12′–28°21′S; 31° 42′–31°59′E) comprises about 47753 ha of hilly country, 130–600 m above sea level. Two vegetation types are recognized, namely Zululand Thornveld along the slopes and crests of the hills and Lowveld in the valleys (Acocks 1988). Both browse and grazing are plentiful. Annual rainfall is 500–750 mm and falls mainly in summer. Summers are hot and winters cool to mild, and frost seldom occurs.

An attempt was made to obtain one adult male, one adult female and one juvenile nyala of either sex at monthly intervals from March 1983 to April 1984, but neither the population sample nor the monthly collection was always possible. Forty nyalas were examined, of which 14 were adult males, 15 adult females, four juvenile males and seven juvenile females. No animals were examined during September or November 1983.

Mkuzi

The Mkuzi Game Reserve, which is approximately 25091 ha in extent, is situated in the so-called Maputaland (27°33′–27°46′S; 32°07′–32°19′E; altitude 130–300 m), and extends from the eastern foothills of the Lebombo mountain range, eastwards into the Makatini flats. The vegetation of the higher areas is classified as Lowveld, while that at lower altitudes consists of the Zululand Palm Veld subdivision of Coastal Forest and Thornveld (Acocks 1988). Rain falls mostly in summer with a variation of 500–750 mm. Summers are hot and often humid and winters are mild. Frost seldom occurs.

Nineteen nyalas were shot from March 1983 to May 1984. Of these, six were adult males, five adult females, five juvenile males and three juvenile females. In addition to these animals three adult male and three adult female nyalas were examined during March 1994.

Ndumu

The Ndumu Game Reserve (26°50′–26°56′S; 32° 09′–32°21′E; altitude 30–100 m) comprises approximately 11000 ha. It is situated in the extreme north of KwaZulu-Natal and shares a common boundary in the north with southern Mozambique. Ndumu falls within the Lowveld subtype of Tropical Bush and Savannah (Acocks 1988). Rainfall varies from 500 to 750 mm per annum and falls mostly in summer. Summers are hot and humid and winters are mild; frost does not occur.

Fourteen nyalas, five adult males, three adult and one old female, one juvenile male and four juvenile females, were shot in this reserve from April 1983 to May 1984.

Collection and counting of parasites

The arthropod parasites of the nyalas were collected, identified and counted as described by Horak, Boomker, Spickett & De Vos (1992) for kudus. The numbers of engorging female ticks were determined only on the six animals examined in Mkuzi during March 1994.

RESULTS

Umfolozi

The ectoparasites collected from animals examined in the Umfolozi Game Reserve are summarized in Table 1.

The nyalas were infested with ten ixodid tick species of which *Rhipicephalus muehlensi*, followed by *Rhipicephalus appendiculatus*, were the most abundant. Every animal was infested with these ticks and with *Boophilus decoloratus*. The nyalas also harboured two louse species and a louse fly.

The seasonal abundances of these ticks and of the immature stages of *Rhipicephalus maculatus* are graphically illustrated in Fig. 1.

The largest numbers of *B. decoloratus* were collected during April and May 1983 and from October 1983 to February 1984. Larvae of *R. appendiculatus* were most abundant from April to October, nymphs from July to October and adults on adult male nyalas during the months of February to May. Larvae of *R. maculatus* were most abundant from May to July and nymphs, from June to October. No clear pattern of seasonal abundance was evident for *R. muehlensi*.

Comment: Observations on the seasonal abundances of all stages of development of *B. decoloratus* and of *R. muehlensi* and the immature stages of *R. appendiculatus* and *R. maculatus* are compromised by the fact that no nyalas were examined during September and November 1983.

Mkuzi

The arthropod burdens of animals examined in this reserve during 1983/1984 and during 1994 are summarized in Tables 2 and 3, respectively.

Eight ixodid tick species were recovered from the first set of nyalas and seven from the second set. Animals examined during the months of October to March generally harboured substantial numbers of *B. decoloratus*, while those examined during May, June and July had very small burdens. The seasonal abundances of *R. appendiculatus* and *R. maculatus* appeared to be similar to those recorded on the nyalas examined in the Umfolozi Game Reserve. *R. muehlensi*, which comprised more than 75% of the

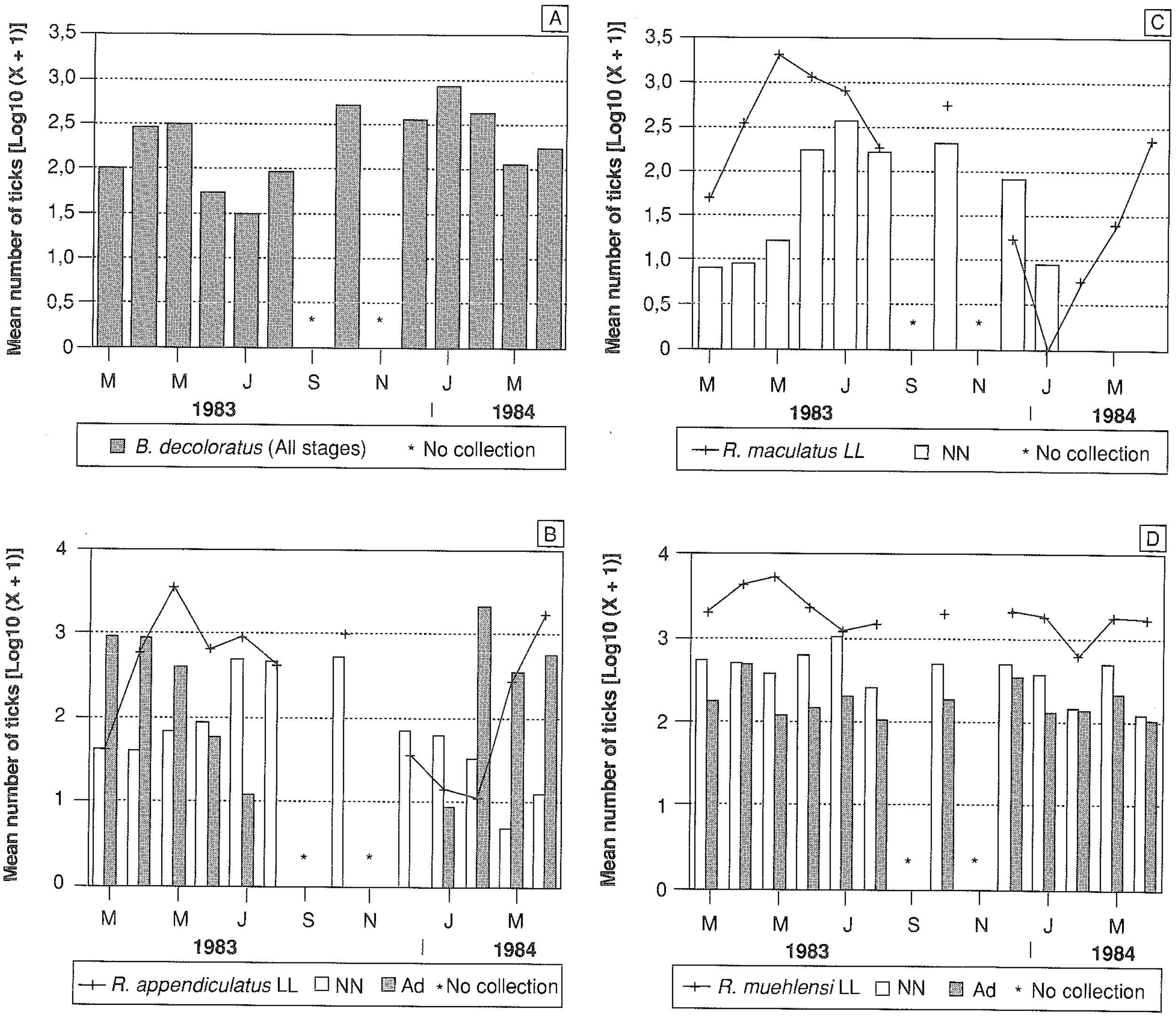

FIG. 1 The seasonal abundance of A. *Boophilus decoloratus*
B. *Rhipicephalus appendiculatus*, (adults only on male animals)
C. *Rhipicephalus maculatus*
D. *Rhipicephalus muehlensi* on nyalas in the Umfolozi Game Reserve

ticks collected from both groups of animals, was present in large numbers throughout the survey.

Most of the nyalas were infested with *Linognathus angasi* and all, with *Lipoptena paradoxa.*

Ndumu

The numbers of arthropods collected from nyalas in this reserve are summarized in Table 4.

The animals were infested with eight ixodid tick species, two species of louse and a louse fly species. *R. muehlensi* was the most abundant and prevalent tick, while considerably fewer *R. appendiculatus* than *R. maculatus* were recovered. The approximately 4-month intervals at which animals were examined, precluded determination of seasonal abundance.

Host sex preference

Twenty-one adult male and 21 adult female nyalas were shot in pairs at the same times and at the same localities during the 1983/1984 survey period. In addition, three adult male and three adult female animals were shot in the Mkuzi Game Reserve on 9–10 March 1994. The parasite burdens of the male and female nyalas were compared by means of the Mann-Whitney *U*-test for non-parametrically distributed data. The mean burdens of the major parasites on these 48 animals are summarized in Table 5.

Adult male nyalas harboured significantly more ($P \leq 0,05$) nymphs of *Amblyomma hebraeum,* males and females of *B. decoloratus, R. appendiculatus* and *R. muehlensi*, males of *R. maculatus,* nymphs and adults of the *Damalinia* sp. and adults of *L. paradoxa* than did adult female nyalas.

Locality preferences

The mean parasite burdens of nyalas examined in each of the reserves during 1983 and 1984 are summarized in Table 6.

Umfolozi was a good habitat for *A. hebraeum*, the only habitat in which *Haemaphysalis silacea* was present, and the only habitat of the three which was more suitable for *R. appendiculatus* than for *R. maculatus.* Mkuzi was a good habitat for *A. hebraeum, B. decoloratus, R. maculatus* and *R. muehlensi.* With the exceptions of *R. muehlensi,* for which it appeared to be the best of the three habitats, and of *R. maculatus*, Ndumu was the least favourable habitat for nearly all tick species. It must, however, be remembered that the animals were not examined in each of the reserves at the same times.

DISCUSSION

Hunters in KwaZulu-Natal often comment on the large numbers of ticks encountered on nyalas. The present findings confirm this observation, particularly as trophy hunters invariably shoot adult male animals and the head and cape (skin of the neck) of the animal are regarded as the trophy. *R. appendiculatus* and *R. muehlensi* prefer the ears, heads and upper necks of male nyalas as attachment sites and are

TABLE 1 Arthropod parasites of 40 nyalas examined in the Umfolozi Game Reserve during 1983/1984

Arthropod species	Total numbers recovered					No. of nyalas infested
Ixodid ticks	Larvae	Nymphs	Males	Females	Total	
Amblyomma hebraeum	16 296	3 030	66	22	19 414	39
Amblyomma spp.	56	0	0	0	56	1
Boophilus decoloratus	4 611	3 225	1 526	1 063	10 425	40
Haemaphysalis aciculifer	0	0	0	2	2	1
Haemaphysalis silacea	571	152	47	60	830	16
Ixodes sp. (near *I. pilosus*)	598	8	14	16	636	11
Rhipicephalus appendiculatus	32 343	7 352	3 160	2 580	45 435	40
Rhipicephalus evertsi evertsi	644	0	10	4	658	15
Rhipicephalus maculatus	20 674	4 183	6	64	24 927	35
Rhipicephalus muehlensi	92 024	19 724	4 662	2 940	119 350	40
Lice	Nymphs		Adults		Total	
Damalinia sp.	2 134		1 269		3 403	13
Linognathus angasi	5 132		2 792		7 924	36
Louse flies	Males		Females		Total	
Lipoptena paradoxa	1 032		1 304		2 360[a]	38

[a] Including pieces of flies whose sex could not be determined

consequently present on those parts of the animal which will ultimately become the trophy. In addition, adults of the latter tick are present throughout the year so that large numbers of ticks are always present on and around the heads of nyalas.

Horak *et al.* (1992) noted that adult male kudus carried significantly more nymphal and adult *A. hebraeum* and adult *B. decoloratus* than did adult females. A similar finding for *L. paradoxa* on kudus was reported by Visagie, Horak & Boomker (1992). These authors postulated that body size, grooming or hormonal influences could be responsible for these differences. If it is assumed that adult male and female nyalas utilize the same habitat, the reasons for the lower tick, louse and louse fly burdens on the females justify further investigation.

Amblyomma spp.

Horak, MacIvor, Petney & De Vos (1987) observed that the larger the host species the greater the likeli-

TABLE 2 Arthropod parasites of 19 nyalas examined in the Mkuzi Game Reserve during 1983/1984

Arthropod species	Total numbers recovered					No. of nyalas infested
Ixodid ticks	Larvae	Nymphs	Males	Females	Total	
Amblyomma hebraeum	7 169	916	28	4	8 117	19
Amblyomma spp.	1 271	0	0	0	1 271	7
Boophilus decoloratus	6 882	1 966	492	214	9 554	18
Ixodes sp. (near *I. pilosus*)	32	0	0	0	32	1
Rhipicephalus appendiculatus	4 650	348	775	645	6 418	18
Rhipicephalus evertsi evertsi	112	8	2	0	122	4
Rhipicephalus maculatus	12 499	1 488	56	58	14 101	19
Rhipicephalus muehlensi	105 491	17 856	7 409	5 238	135 994	19
Lice	Nymphs		Adults		Total	
Damalinia sp.	112		104		216	4
Linognathus angasi	1 492		562		2 054	17
Louse flies	Males		Females		Total	
Lipoptena paradoxa	354		414		798[a]	19

[a] Including pieces of flies whose sex could not be determined

TABLE 3 Arthropod parasites of six nyalas examined in the Mkuzi Game Reserve during March 1994

Arthropod species	Total numbers recovered					No. of nyalas infested
Ixodid ticks	Larvae	Nymphs	Males	Females	Total	
Amblyomma hebraeum	2 620	274	24	4	2 922	6
Amblyomma spp.	81	0	0	0	81	2
Boophilus decoloratus	1 785	375	160	146 (16)	2 466	6
Rhipicephalus appendiculatus	8	0	975	535 (22)	1 518	6
Rhipicephalus evertsi evertsi	48	0	11	2	61	5
Rhipicephalus maculatus	220	19	14	14	267	6
Rhipicephalus muehlensi	30 880	4 351	3 235	2 092 (190)	40 558	6
Lice	Nymphs		Adults		Total	
Damalinia sp.	222		55		277	3
Linognathus angasi	639		232		871	6
Louse flies	Males		Females		Total	
Lipoptena paradoxa	295		403		704[a]	6

( ) = Number of engorging female ticks, i.e. idiosoma of *B. decoloratus* and *R. muehlensi* > 4,0 mm and *R. appendiculatus* > 5,0 mm in length

[a] = Including pieces of six flies whose sex could not be determined

TABLE 4 Arthropod parasites of 14 nyalas examined in the Ndumu Game Reserve during 1983/1984

Arthropod species	Total numbers recovered					No. of nyalas infested
Ixodid ticks	Larvae	Nymphs	Males	Females	Total	
Amblyomma hebraeum	224	190	0	0	414	9
Amblyomma spp.	48	0	0	0	48	2
Boophilus decoloratus	388	164	66	36	654	10
Ixodes sp. (near *I. pilosus)*	48	32	2	0	82	3
Rhipicephalus appendiculatus	2 888	196	234	176	3 494	12
Rhipicephalus evertsi evertsi	32	0	0	0	32	1
Rhipicephalus maculatus	10 000	734	86	56	10 876	13
Rhipicephalus muehlensi	93 764	17 724	6 370	4 176	122 034	14
Lice	Nymphs		Adults		Total	
Damalinia sp.	24		48		72	2
Linognathus angasi	1 968		616		2 584	12
Louse flies	Males		Females		Total	
Lipoptena paradoxa	368		452		822[a]	12

[a] Including pieces of two flies whose sex could not be determined

hood that it would harbour large numbers of adult *A. hebraeum*. From a subsequent study it would appear as if kudus lie on the border between the really large and the smaller wild-host species (Horak *et al.* 1992). Male kudus may harbour fairly substantial numbers of adult *A. hebraeum,* while females seldom carry more than two or three ticks. Although both the Umfolozi and Mkuzi Game Reserves are located in habitats favourable for *A. hebraeum*, not all animals were infested with adults, and the largest burden of adult *A. hebraeum* comprised only 22 ticks, which incidently were recovered from an adult female nyala. This indicates that nyalas fall within the group of smaller host species, i.e. they are good hosts of the immature stages but not of adult *A. hebraeum.*

The absence of a pattern of seasonal abundance can be ascribed to the year-round warm climate of the reserves, similar to that encountered in the Kruger National Park, where all stages of *A. hebraeum* were present on kudus throughout the year (Horak *et al.* 1992).

Both *Amblyomma marmoreum* and *Amblyomma nuttalli,* whose adults prefer to feed on tortoises, are present in KwaZulu-Natal (Walker 1991). We are unable to differentiate between the immature stages of these ticks and have therefore allocated specimens resembling them, merely to *Amblyomma* spp. Most of these ticks were collected from nyalas in the Mkuzi Game Reserve and were present mainly during March.

Boophilus decoloratus

Substantial numbers of this tick have been recorded on cattle at lower altitudes in southern KwaZulu-Natal (Baker & Ducasse 1967; Baker *et al.* 1989). Although Baker & Keep (1970) list it as occurring on numerous wild animals, including nyalas, in this province, quantitative studies by Horak *et al.* (1983, 1988, 1989, 1991a) indicate that it is present only in small numbers on wild animals in those regions where the latter authors conducted their studies. In the present survey, however, nyalas in the Mkuzi Game Reserve harboured fairly large numbers of *B. decoloratus*. The overall ratio of larvae to nymphs to adults of 3,7:1,5:1,0, calculated from all the nyalas examined, is not unlike that found on kudus in the Eastern Transvaal (3,0:2,0:1,0) and implies a good translation of larvae and nymphs to adulthood (Horak *et al.* 1992). With the exception of two localities at which tick numbers increased in spring, Baker *et al.* (1989) recorded the largest burdens of *B. decoloratus* on cattle from mid to late summer or autumn. In this survey, the largest burdens were present on nyalas examined in months falling within the period October to May (spring to autumn).

Haemaphysalis spp.

Baker & Keep (1970) recorded *H. aciculifer* on common duikers, common reedbuck and bushbuck in the Umfolozi/Hluhluwe Game Reserve complex, and Horak *et al.* (1989) collected this tick from common duikers and bushbuck in the Weza State Forest, southern KwaZulu-Natal. Although *H. aciculifer* is widely distributed, it is never encountered in very large numbers (Walker 1991). It was collected from only one nyala in this study.

H. silacea has been recorded on animals in the Umfolozi/Hluhluwe Game Reserve complex and in the

TABLE 5 A comparison of the parasite burdens of 24 male and 24 female nyalas examined at the same localities in north-eastern KwaZulu-Natal at the same times

Developmental stage	Male nyalas		Female nyalas		Significance $P \leq 0,05$
	Mean burden (range)	No. of nyalas infested	Mean burden (range)	No. of nyalas infested	
Ixodid ticks					
Amblyomma hebraeum					
Larvae	503,5 (0–1 866)	21	282,3 (0–1 135)	21	–
Nymphs	114,0 (0–368)	21	41,5 (0–160)	20	0,020
Males	2,7 (0–10)	14	1,9 (0–20)	7	–
Females	0,8 (0–4)	8	0,5 (0–10)	2	–
Boophilus decoloratus					
Larvae	186,6 (0–1 157)	19	124,2 (0–464)	21	–
Nymphs	106,3 (0–596)	17	57,1 (0–256)	18	–
Males	61,4 (0–504)	20	18,9 (0–128)	14	0,030
Females	43,3 (0–344)	22	9,7 (0–76)	15	0,005
Rhipicephalus appendiculatus					
Larvae	517,3 (0–3 746)	18	605,5 (0–5 421)	17	–
Nymphs	144,1 (0–912)	14	88,3 (0–560)	15	–
Males	194,2 (0–1 232)	17	4,9 (0–30)	10	0,002
Females	150,4 (0–1 030)	16	2,5 (0–20)	10	0,005
Rhipicephalus maculatus					
Larvae	419,3 (0–3 276)	20	480,2 (0–1 929)	18	–
Nymphs	92,5 (0–448)	17	82,7 (0–448)	18	–
Males	3,8 (0–42)	10	0,0 (0)	0	0,010
Females	6,4 (0–44)	8	0,7 (0–16)	1	–
Rhipicephalus muehlensi					
Larvae	3 561,8 (448–12 564)	24	3 833,2 (762–8 875)	24	–
Nymphs	625,9 (28–3 712)	24	662,2 (0–2 046)	23	–
Males	389,3 (78–1 239)	24	174,2 (14–555)	24	0,002
Females	256,4 (36–1 152)	24	117,5 (10–351)	24	0,010
Lice					
Damalinia sp.					
Total	159,8 (0–2 044)	17	2,0 (0–32)	2	0,001
Linognathus angasi					
Total	156,2 (0–1 056)	22	248,7 (0–3 504)	20	–
Louse flies					
Lipoptena paradoxa					
Adults	114,0 (28–340)	24	37,6 (0–220)	23	0,001

TABLE 6 The mean total arthropod parasite burdens of nyalas examined in the Umfolozi, Mkuzi and Ndumu Game Reserves during 1983/1984

Arthropod species	Mean total burdens per species		
	Umfolozi (40)	Mkuzi (19)	Ndumu (14)
Ixodid ticks			
Amblyomma hebraeum	485	427	30
Amblyomma spp.	1	67	3
Boophilus decoloratus	261	503	47
Haemaphysalis silacea	21	0	0
Ixodes sp. (near *I. pilosus*)	16	2	6
Rhipicephalus appendiculatus	1 136	338	250
Rhipicephalus evertsi evertsi	16	6	2
Rhipicephalus maculatus	623	742	777
Rhipicephalus muehlensi	2 984	7 158	8 717
Lice			
Damalinia sp.	85	11	5
Linognathus angasi	198	108	185
Louse flies			
Lipoptena paradoxa	59	42	59

( ) = Number of animals examined in each reserve

Mkuzi Game Reserve by Baker & Keep (1970), but we collected it only in the Umfolozi Game Reserve. The preferred habitat of this tick is localized areas of Valley Bushveld in the Eastern Cape Province (Walker 1991), where large numbers have been recorded on kudus (Horak *et al.* 1992).

Ixodes pilosus complex

McKay (1994) believes that there are three separate species in this complex. Although *I. pilosus* sensu stricto does occur in KwaZulu-Natal (McKay 1994), the nyalas in the present study harboured adult ticks which he describes as "thick haired *pilosus*".

Rhipicephalus spp.

The adults of *R. appendiculatus* prefer large bovids such as cattle, eland and buffaloes, but kudus, sable antelope and impalas are also good hosts (Norval, Walker & Colborne 1982; Horak *et al.* 1983, 1992). Adult male, but not female, nyalas can now be added to this list. Six male animals each harboured more than 600 adult ticks and one of them, 2262 ticks.

Baker & Ducasse (1967) recovered 69,3% of adult *R. appendiculatus* from the ear pinnae of cattle and 80,0% from the pinnae and the remainder of the cattle's heads. The three male nyalas examined in the Mkuzi Game Reserve during 1994 harboured a total of 1461 adult *R. appendiculatus* of which 520 (35,6%) attached on their heads and ears. This distribution pattern could be the result of competition with the numerous adult *R. muehlensi* which were also present. The male nyalas harboured a total of 3428 of these, of which 2316 (67,6%) were attached to their heads and ears. The three female nyalas examined at the same time, harboured a total of 49 adult *R. appendiculatus* and 1899 adult *R. muehlensi,* of which 57,1% and 91,0%, respectively, were attached to their heads and ears.

The period of peak abundance of *R. appendiculatus* on the male nyalas (February to May) is the same as that recorded on kudus in north-eastern Eastern Transvaal (Horak *et al.* 1992).

R. evertsi evertsi has a very widespread distribution in South Africa (Howell, Walker & Nevill 1978) but, except on zebras and eland, the adults never occur in very large numbers (Horak, Fourie, Novellie & Williams 1991b). Nyalas, like kudus, appear to be poor hosts of this tick (Horak *et al.* 1992). Not only were few adults collected, but very few larvae of this two-host tick developed into nymphs.

Within the South African borders, *R. maculatus* is present in the coastal regions of KwaZulu-Natal (Walker 1991). The adults prefer large animals with thick skins, such as elephants, black and white rhinoceroses, buffaloes, bushpigs and warthogs (Baker & Keep 1970; Horak *et al.* 1983, 1991a). Excluding elephants, the immature stages are also found on these hosts as well as on various duiker species, reedbuck, impalas, and particularly on nyalas, also on scrub hares (Baker & Keep 1970; Horak *et al.* 1983, 1988, 1991a, 1995). The seasonal abundances of the immature stages are similar to those of *R. appendiculatus.*

Nyalas, and probably also bushbuck, must be regarded as the preferred hosts of all developmental stages of *R. muehlensi* (Horak *et al.* 1983, 1988; this study). This tick, like *R. maculatus,* is present in South Africa only in the coastal regions of northern KwaZulu-Natal (Walker 1991). Large numbers of nymphs, and probably also larvae (which at the time were lumped with other larvae and identified as *Rhipicephalus* spp.), have been recovered from red duikers and numerous larvae from scrub hares (Horak *et al.* 1991a, 1995). Nyalas, bushbuck and red duikers are all browsers and are found in habitats containing thickets, various types of woodland or forests, while scrub hares prefer savanna woodland and scrub (Smithers 1983).This implies that *R. muehlensi* also prefers these habitat types.

The large totals of these ticks recovered from nyalas, reflect the year-round abundance of all developmental stages of *R. muehlensi.* As discussed earlier, competition with adult *R. appendiculatus* may affect the proportion of adult *R. muehlensi* attaching to the heads and ears of nyalas.

Lice

With few exceptions, louse burdens were low, and adult male animals harboured significantly more *Damalinia* sp. than did adult females. No pattern of seasonal abundance was evident for either of the louse species.

Louse flies

The biology of *L. paradoxa*, with particular reference to kudus, was discussed by Visagie *et al.* (1992). The preferred hosts of this fly are all browsing antelopes, namely common duikers, bushbuck, nyalas and kudus. Adult male kudus and nyalas harbour significantly more of these flies than do adult female animals (Visagie *et al.* 1992; Table 5). Visagie *et al.* (1992) collected 3 594 flies whose sex could be determined, from common duikers, bushbuck and kudus. Of these flies 2 243 (62,4%) were females. In the present study 4622 *L. paradoxa* whose sex could be determined were collected, and 2573 (55,7%) of these were females.

ACKNOWLEDGEMENTS

This study is part of the Wildlife Research Programme of the Faculty of Veterinary Science, University of Pretoria.

The Natal Parks Board is thanked for placing the nyalas at our disposal, and we greatly appreciate the assistance of the staff of the three game reserves with the necropsies. Dr J.P. Louw, Mr E.J. Williams and Mr A.C. Uys assisted with the collection of parasites from the animals or from the processed material and Dr I.J. McKay, with the identification of the *Ixodes* sp. Miss Andrea van Niekerk constructed the figures.

This research was funded by the Foundation for Research Development.

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S. Afr. J. Wildl. Res. 1997, 27(1)

A ten-year study of ixodid tick infestations of bontebok and grey rhebok in the Western Cape Province, South Africa

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Received 16 August 1996; accepted 3 October 1996

Two to four bontebok *Damaliscus pygargus dorcas* and three to four grey rhebok *Pelea capreolus*, in the Bontebok National Park, Western Cape Province, South Africa, were examined for ticks during February of each year from 1983 to 1992. A total of 34 bontebok and 37 grey rhebok were examined. The bontebok harboured eight ixodid tick species of which *Rhipicephalus glabroscutatum* and *Rhipicephalus nitens* were the most abundant. The grey rhebok harboured six species of which the former two ticks and *Ixodes pilosus* were the most numerous. With the exception of 1986 and 1989, when *R. glabroscutatum* was most abundant on the bontebok and grey rhebok respectively, and 1985 when *I. pilosus* was most plentiful on the grey rhebok, *R. nitens* was the most abundant tick species on both host species. Despite *Boophilus microplus* being present on animals outside the Park, as well as the translocation of Cape mountain zebras *Equus zebra zebra* and red hartebeest *Alcelaphus buselaphus* to the Park, no foreign tick species became established on the two hosts during the 10 years of observation. Nor did any of the tick species present only in low numbers become more plentiful.

Keywords: bontebok, grey rhebok, ixodid ticks, 10-year study

Introduction

The adverse effects, including mortality, of ticks on wild artiodactylids, are well documented (Lightfoot & Norval 1981; Melton 1987; Fourie & Vrahimis 1989). The nature and extent of host injury are dependent on the tick species and burdens (Lightfoot & Norval 1981; Fourie & Kok 1992). In order to anticipate such tick-related problems it is important to determine the status of wild animals as hosts for the various tick species which infest them. Several abiotic and biotic factors may affect tick burdens (Randolph 1994) and may also influence the various tick species differently (Theiler 1970). This implies that species which are dominant during a particular year may occur in lower numbers during subsequent years and *vice versa.* In addition translocation of animals or physical alteration of the environment may result in ticks and the diseases they transmit becoming established in regions in which they did not occur historically (Barré, Uilenberg, Morel & Camus 1987; Spickett & Heyne 1988). Such dynamic changes can only be established by long-term studies.

During 1983–84 a survey was conducted to quantify the arthropod parasites, particularly ticks, of bontebok *Damaliscus pygargus dorcas*, grey rhebok *Pelea capreolus* and scrub hares *Lepus saxatilis* in the Bontebok National Park (Horak, Sheppey, Knight & Beuthin 1986b). Nine ixodid tick species were collected from both bontebok and grey rhebok, whilst the scrub hares harboured 11 species. The ticks *Rhipicephalus glabroscutatum* and *Rhipicephalus nitens* were considered to be the definitive parasites of bontebok, *R. nitens* and *Ixodes pilosus* those of grey rhebok and *R. nitens* of scrub hares (Horak *et al.* 1986b). Two *Boophilus* nymphs were collected from the grey rhebok and five from scrub hares. A grey rhebok examined immediately outside the borders of the Park, however, harboured small numbers of *Boophilus microplus* and of *B. decoloratus.* This implied a potential for these ticks to become established in greater numbers within the Park.

During the present study ticks infesting bontebok and grey rhebok in the Bontebok National Park were collected over a period of 10 years. The objectives were to ascertain whether any foreign tick species became established in the Park and also to determine possible changes in the relative abundance of the ticks parasitizing the two host species.

Methods

Study site

The Bontebok National Park (34°02'S;20°25'E; alt. 90–200 m) encompasses 2803 ha and is situated in the southern Western Cape Province, South Africa. The vegetation, which forms part of the Cape macchia, is described as Coastal Renosterbosveld (Acocks 1988) and the Park topography consists of a series of gravel terraces gradually rising to the north-eastern corner. Sand flats, surrounded by low hills occur in the south-west (Theron 1967). Wildlife census results for the Park during the year preceding and for the 10 years of the survey are summarized in Table 1. During this period the bontebok and grey rhebok numbers were stabilized

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Table 1 Wildlife counts in the Bontebok National Park, 1982–1992

		Numbers of animals counted		
Year	Month	Bontebok	Grey rhebok	Other species
1982	March	352	160	Springbok 16
1983	February	279	181	
1984	February	305	175	Grysbok 17; Steenbok 12
	September	232	148	
1985	January	274	180	Grysbok 15; Steenbok 18
	September	239	173	
1986	February	285	207	Grysbok 24; Steenbok 14
	September	268	211	
1987	June	208	153	
	September	215	122	
1988	January	253	112	
	June	178	185	Red hartebeest 5; Mountain zebra 2
	October	192	197	
1989	August	205	128	Red hartebeest 7; Mountain zebra 2
1990	January	256	142	
	August	198	64	Red hartebeest 8; Mountain zebra 5
1991	February	206	106	
	April	203	156	
	May	231	147	
	September	233	102	Red hartebeest 10; Mountain zebra 8
1992	February	252	95	Red hartebeest 13; Mountain zebra 11

or reduced by culling and by translocation. Cape mountain zebras *Equus zebra zebra* and red hartebeest *Alcelaphus buselaphus* were introduced during 1988 and their numbers increased naturally and by further translocations. Although steenbok *Raphicerus campestris* and Cape grysbok *Raphicerus melanotis* were not counted during 1983 or subsequent to 1986 it can be assumed that the numbers of these small antelopes remained fairly constant. Rainfall was recorded daily in the Park.

Survey animals

During February of each year from 1983 to 1992 two to four bontebok and three to four grey rhebok were shot for survey purposes. The animals examined during February of 1983 and of 1984 in the previously mentioned survey (Horak *et al.* 1986b) have been included in this survey for those years.

Parasite recovery and counting

The skins of the animals were processed for arthropod parasite recovery as described by Horak, Boomker, Spickett & De Vos (1992) and the parasites identified and counted under a stereoscopic microscope.

The lungs, livers and gastro-intestinal tracts of the antelopes were processed for the recovery of helminths. These findings will be reported separately, as will those of the arthropods other than ticks recovered from the animals.

Results

A total of 34 bontebok and 37 grey rhebok were examined. The ticks infesting the two hosts are summarized in Tables 2 & 3. Eight species were collected from bontebok of which *Boophilus* sp., *Haemaphysalis aciculifer*, *R. evertsi evertsi* and *Hyalomma truncatum* were present only occasionally and in very low numbers (Table 2). Six species were collected from grey rhebok, with *H. aciculifer* and *R. evertsi evertsi* present in low numbers and only infrequently (Table 3).

The relative abundances of the major tick species infesting the two hosts are graphically presented in Figures 1 & 2. Large variations in relative abundance were recorded during the 10 year study period. The relative abundance of *R. glabroscutatum* on the bontebok increased steadily from 1984, reached a peak (58%) during 1986 and declined to its lowest level (0.5%) during 1991 (Figure 1). *R. nitens* was the most abundant tick during nine of the 10 years (Figure 1). On grey rhebok, *I. pilosus* displayed the highest relative abundance during 1985 and *R. glabroscutatum* during 1989. During the other years *R. nitens* was the dominant species (Figure 2).

Discussion

The diversity of tick species which occurred on the two hosts during the 10 years of observation stayed the same. None of the ticks which were previously collected in low numbers by Horak *et al.* (1986b) became more abundant.

One of the ways in which ticks are introduced into new areas is by host translocation (Braack, Maggs, Zeller & Horak 1995). Either the ticks that were present on the Cape mountain zebras and red hartebeest when they were introduced into the Bontebok National Park during 1988 did not survive in the new habitat, or their numbers are still too low to be detected on other hosts. The zebras and hartebeest could potentially serve as hosts for *Boophilus* spp., *Hyalomma truncatum* and *R. evertsi evertsi.* Mountain zebras are particularly good hosts of the latter two ticks and of *Margaropus winthemi*, the dominant species in the mountainous regions from which these animals came (Horak, Knight & De Vos 1986a).

The relative abundance of the various tick species on the hosts displayed long-term fluctuations. These fluctuations were chiefly caused by considerable variations in the numbers of the immature stages of *R. glabroscutatum*, a two-host tick, and the larvae of *I. pilosus* and of *R. nitens*, both three-host species. The fluctuations could be associated with climatic factors which affect the various tick species differently, or which affect the vegetation, causing the animals to feed in different localities to those normally utilized at a particular time of the year. Analysis of individual tick species indicated that all stages of development of *R. glabroscutatum* appeared to decrease on the bontebok from February 1985 to February 1991 and the adults of *R. nitens* from 1984 until 1990. The adults of the latter tick also decreased, albeit erratically, on the grey rhebok from 1984 and 1985 to 1991. In the case of *R. nitens*, where the adult ticks attach to the ears and lower jaws, and of *I. pilosus*, of which the adult ticks attach to the head and body, intraspecific or interspecific competition (Andrews & Petney 1981; Petney & Al-Yaman 1985) for the site of attachment may also influence population size. The implication is

Table 2 Ixodid ticks collected from bontebok in the Bontebok National Park during February of each year from 1983–1992

Year	*Amblyomma marmoreum*				*Boophilus sp.*				*Haemaphysalis aciculifer*				*Hyalomma truncatum*				*Ixodes pilosus*				*Rhipicephalus e. evertsi*				*Rhipicephalus glabroscutatum*				*Rhipicephalus nitens*			
	L	N	♂	♀	L	N	♂	♀	L	N	♂	♀	L	N	♂	♀	L	N	♂	♀	L	N	♂	♀	L	N	♂	♀	L	N	♂	♀
1983																																
x	4.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9.0	0	0	1.0	0	0	0	0	22.0	4.0	2.0	0	666.0	5.0	3.0	3.5
SD	2.8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12.7	0	0	1.4	0	0	0	0	22.6	2.8	2.8	0	169.7	4.2	1.4	4.9
1984																																
x	1.0	0	0	0	0	0	0	0	0	0	0	1.0	0	0	0	0	12	1.5	0	0	0	0	0	0	60.0	9.5	0	0	140.0	1.0	27.5	42.0
SD	1.4	0	0	0	0	0	0	0	0	0	0	1.4	0	0	0	0	2.8	2.1	0	0	0	0	0	0	70.7	7.8	0	0	65.1	1.4	24.7	48.1
1985																																
x	2.7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3.3	0.7	0	0.7	0	8.7	0	0	357.0	32.7	2.7	1.3	564.0	14.0	20.7	27.0
SD	4.6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.2	1.2	0	1.2	0	9.0	0	0	349.9	22.5	2.5	1.5	387.0	15.1	15.6	26.6
1986																																
x	0.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.0	1.5	0	0.5	0	0	0	0	242.5	10.0	0.5	1.0	148.0	2.5	14.0	17.5
SD	1.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.3	1.9	0	1.0	0	0	0	0	446.7	14.9	1.0	1.2	96.7	3.0	10.1	10.0
1987																																
x	8.7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.7	0.7	0	0	0	0	0	0	19.3	38.7	0	0.7	42.0	2.0	11.3	12.3
SD	15.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.2	1.2	0	0	0	0	0	0	15.0	60.2	0	1.2	10.6	2.0	8.4	9.7
1988																																
x	3.5	0	0	0	0	0	0	0	1.0	0	0	0	0	0	0	0	0.5	0.5	0.5	0	2.0	0	0	0	4.0	5.5	0.5	0.5	92.0	1.0	7.5	7.0
SD	5.7	0	0	0	0	0	0	0	2.0	0	0	0	0	0	0	0	1.0	1.0	1.0	0	2.8	0	0	0	6.7	11.0	1.0	1.0	118.1	2.0	3.4	3.8
1989																																
x	1.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7.8	6.8	0	1.3	101.0	0.5	7.8	6.8
SD	1.7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9.7	9.9	0	1.5	97.1	0.6	5.7	5.6
1990																																
x	0	0	0	0	1.0	0	0	0	0	0	0	0	0	0	0	0	3.0	0.5	0	0	0	0	0	0	6.0	0	0	0	272.5	1.0	7.0	1.0
SD	0	0	0	0	2.0	0	0	0	0	0	0	0	0	0	0	0	6.0	1.0	0	0	0	0	0	0	1.6	0	0	0	81.4	1.2	6.2	1.2
1991																																
x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.0	0	0	0	191.5	1.5	7.3	7.0
SD	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.2	0	0	0	177.1	1.9	8.4	5.3
1992																																
x	1.0	0	0	0	0	0	0	0	0	0	0	0	0.5	0	0	0	4.0	1.0	0	0	0	0.5	0	0	17.5	7.0	1.0	2.5	615.0	9.0	19.0	19.3
SD	2.0	0	0	0	0	0	0	0	0	0	0	0	1.0	0	0	0	4.9	1.2	0	0	0	1.0	0	0	21.7	8.7	2.0	3.0	658.4	7.6	14.3	10.3

Table 3 Ixodid ticks collected from grey rhebok in the Bontebok National Park during February of each year from 1983–1992

Year	*Amblyomma marmoreum*				*Haemaphysalis aciculifer*				*Ixodes pilosus*				*Rhipicephalus evertsi evertsi*				*Rhipicephalus glabroscutatum*				*Rhipicephalus nitens*			
	L	N	♂	♀	L	N	♂	♀	L	N	♂	♀	L	N	♂	♀	L	N	♂	♀	L	N	♂	♀
1983																								
x	9.0	0	0	0	0	0	0	0.3	36.5	4.0	1.0	3.5	0	0	0	0	1.0	0	1.0	0	155.5	4.5	15.8	21.8
SD	13.2	0	0	0	0	0	0	0.5	15.1	4.3	0.8	4.1	0	0	0	0	2.0	0	1.2	0	163.5	4.1	20.8	22.5
1984																								
x	1.0	0	0	0	0	0	0	0	2.0	3.0	0.3	4.8	0	0	0.5	0	4.5	0	0.5	0.5	32.0	0	20.3	26.8
SD	2.0	0	0	0	0	0	0	0	2.8	4.8	0.5	3.6	0	0	1.0	0	5.7	0	1.0	1.0	38.1	0	16.8	22.2
1985																								
x	6.7	0	0	0	0	0	0	0	148.0	12.7	1.7	5.7	0	0	0	0	4.0	14.0	0.7	0.7	52.0	0.7	4.3	10.0
SD	3.1	0	0	0	0	0	0	0	126.6	12.1	0.6	2.5	0	0	0	0	2.0	22.5	1.2	1.2	84.9	1.2	2.9	4.6
1986																								
x	2.7	0	0	0	0	0	0	0	2.7	0.7	0	0.7	0	0	0	0	0	0	0	0	0.7	0	2.0	1.3
SD	4.6	0	0	0	0	0	0	0	4.6	1.2	0	1.2	0	0	0	0	0	0	0	0	1.2	0	2.0	1.2
1987																								
x	2.7	0	0	0	0	0	0	0	7.3	2.0	0	1.7	2.0	0.7	0	0.3	2.0	0	4.0	1.3	157.3	0	12.7	16.7
SD	3.1	0	0	0	0	0	0	0	12.7	2.0	0	1.5	3.5	1.2	0	0.5	3.5	0	3.5	1.6	231.6	0	10.0	17.7
1988																								
x	0	0	0	0	0	0	0	0	0.5	0	0.3	0	0	0	0	0	5.0	0.5	0.5	0.5	31.0	0	5.3	12.8
SD	0	0	0	0	0	0	0	0	1.0	0	0.5	0	0	0	0	0	7.6	1.0	1.0	1.0	12.5	0	4.3	11.2
1989																								
x	1.0	0	0	0	0	0	0	0	1.0	0.5	0	0.3	0.3	0	0	0	60.5	3.0	1.0	0.3	31.5	0.3	2.5	0.5
SD	2.0	0	0	0	0	0	0	0	1.4	1.0	0	0.5	0.5	0	0	0	77.1	4.1	1.4	0.5	42.4	0.5	1.7	0.6
1990																								
x	0	0	0	0	0	0	0	. 0	7.5	2.5	0.5	3.5	0	0	0	0	3.0	2.5	0	0	37.0	0	1.5	0.5
SD	0	0	0	0	0	0	0	0	9.0	3.0	1.0	3.4	0	0	0	0	6.0	3.8	0	0	42.4	0	3.0	1.0
1991																								
x	0	0	0	0	0	0	0	0.5	6.0	0.5	1.0	0.5	0	0	0	0	0	1.5	0	0	24.5	0	0	0.5
SD	0	0	0	0	0	0	0	1.0	4.9	1.0	2.0	1.0	0	0	0	0	0	3.0	0	0	39.7	0	0	1.0
1992																								
x	4.0	0	0	0	0	0	0	0	50.0	0.5	0.3	2.3	1.0	5.5	0	0	128.0	2.0	0	1.0	353.0	2.0	3.0	5.3
SD	8.0	0	0	0	0	0	0	0	80.1	1.0	0.5	1.5	2.0	11.0	0	0	244.0	4.0	0	2.0	446.6	4.0	2.4	8.5

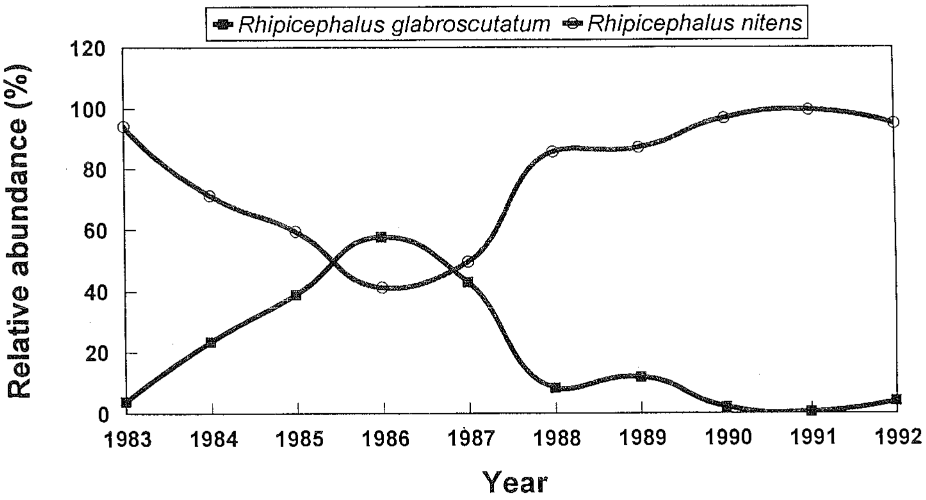

Figure 1 The relative abundance of the major tick species which infested bontebok in the Bontebok National Park as determined during February of 1983–1992.

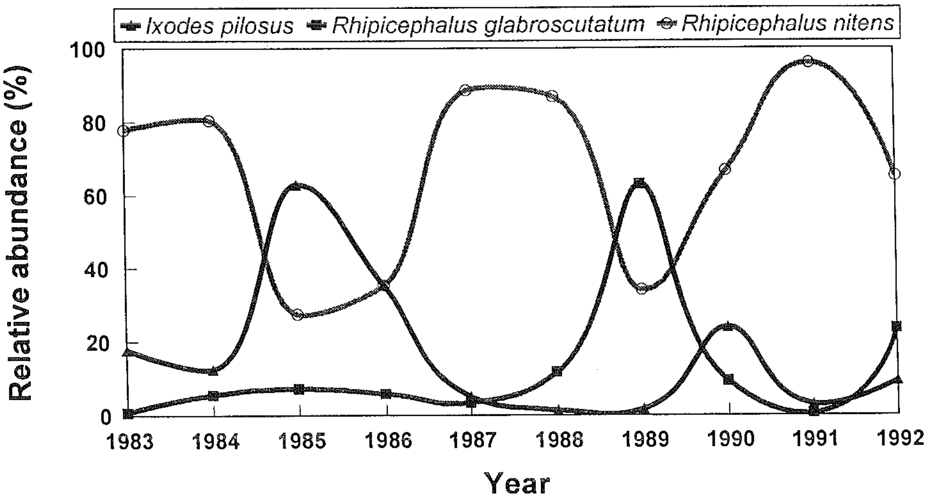

Figure 2 The relative abundance of the major tick species which infested grey rhebok in the Bontebok National Park as determined during February of 1983–1992.

that ticks attaching to non-preferential feeding sites may be removed more easily by the grooming actions of the host.

In terms of general tick ecology and host-tick interactions the results obtained during this long-term study are important for a number of reasons. Firstly, they illustrate the dynamic nature of tick populations on hosts in which a tick species, which is most abundant during a particular year, may not necessarily be so during subsequent years. This demonstrates the danger of determining relative species abundance for a region from a once-off collection, even though the latter may involve the examination of a number of endemic host species. This applies even more so in a stock-farming situation where several tick species may be more severely affected than others by acaricidal intervention.

Secondly, in terms of the epidemiology of tick-transmitted diseases, the population size of certain disease-inducing tick species may increase gradually until critical levels are reached, and hosts are affected. Karoo paralysis, caused by *Ixodes rubicundus*, is a pertinent example where a specific infestation level is required before paralysis is induced (Fourie & Horak 1987; Fourie & Vrahimis 1989). *R. nitens* may also cause a tick toxicosis similar to that recorded in cattle for *Rhipicephalus appendiculatus* by Thomas & Neitz (1958). Springbok *Antidorcas marsupialis* in the southern Western Cape Province, infested with large numbers of *R. nitens* during February, have been severely affected and have died (Horak, unpublished data). Whether this is also the case for bontebok and grey rhebok in the study area is unknown.

Furthermore, if drastic increases in total tick burdens were noted during a long-term study these could indicate management problems. This is particularly true in small nature reserves where overstocking could lead to territorial or nutritional stress or into which too many individuals of tick susceptible host species had been introduced during translocation operations. Finally, such studies could indicate whether non-endemic tick species had been introduced and become established in a particular habitat over a period of years.

Despite *B. microplus* being fairly widespread in South Africa (Howell, Walker & Nevill 1978), the recovery of small numbers of this tick from a single grey rhebok grazing in a paddock with cattle outside the perimeter of the Park by Horak *et al.* (1986b), is the only record on a wild host in this country from the more than 1000 potentially suitable wild ruminant and equid hosts examined over a period of some 20 years by one of us (I.G.H.). Consequently its continued absence in the Park in spite of cattle grazing up to the boundary fences is not unexpected.

Acknowledgements

This study is part of the Wildlife Research Programme of the Faculty of Veterinary Science, University of Pretoria. We wish to thank the National Parks Board for placing the antelopes at our disposal, and the Park wardens and their staff for assisting with the necropsies. The project was funded by the Foundation for Research Development, the University of Pretoria and Rhodes University.

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Onderstepoort Journal of Veterinary Research, 65:205–211 (1998)

Parasites of domestic and wild animals in South Africa. XXXV. Ixodid ticks and bot fly larvae in the Bontebok National Park

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ABSTRACT

HORAK, I.G. & BOOMKER, J. 1998. Parasites of domestic and wild animals in South Africa. XXXV. Ixodid ticks and bot fly larvae in the Bontebok National Park. *Onderstepoort Journal of Veterinary Research*, 65:205–211

Ixodid ticks were collected during February of each year from 1983–1992 from bontebok and grey rhebok in the Bontebok National Park, Western Cape Province. When available other mammals as well as ground-nesting birds and leopard tortoises were examined. Eleven tick species were recovered. *Rhipicephalus nitens* followed by *Rhipicephalus glabroscutatum* and an *Ixodes* sp. (near *I. pilosus*) were the most abundant, while *Amblyomma marmoreum* infested the widest host range.

The larvae of three bot flies were also collected. *Gedoelstia* sp. and *Strobiloestrus* sp. larvae were recovered from bontebok and grey rhebok and larvae of *Oestrus ovis* only from grey rhebok.

Keywords: Birds, bontebok, Bontebok National Park, bot fly larvae, grey rhebok, hares, ixodid ticks, rodents, tortoises

INTRODUCTION

A bi-monthly study, lasting 13 months, of some of the arthropods infesting animals in the Bontebok National Park, Western Cape Province, South Africa, has already been conducted (Horak, Sheppey, Knight & Beuthin 1986b). That survey was carried out to ascertain not only the arthropod species, particularly ixodid ticks and bot fly larvae, parasitizing animals in the Park but also their seasonal abundances. The present study extended the scope of the previous one by including ground-nesting birds and tortoises. It also looked at possible changes that might have occurred in tick burdens of bontebok and grey rhebok over a period of 10 years. The latter aspect has been addressed in a separate publication (Horak, Fourie & Boomker 1997).

MATERIALS AND METHODS

Study locality

The study was conducted on animals resident in the Bontebok National Park (34°02'S, 20°25'E). The physiography of this park has previously been described by Boomker, Horak & De Vos (1981).

Survey period

Animals were examined during February of each year over a period of 10 years from 1983–1992. The animals examined during February 1983 and 1984 in the earlier study conducted by Horak *et al.* (1986b) have been included in this survey as being the first 2 years of the 10-year period.

Survey animals

The mammal, bird and tortoise species and the numbers of each examined are summarized in Table 1.

The species examined comprised two ruminants, two rodents, a hare, three ground-nesting birds and the leopard tortoise. The larger mammals and birds were

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Accepted for publication 22 June 1998—Editor

TABLE 1 Mammals, birds and reptiles examined for ixodid ticks in the Bontebok National Park

Common name	Specific name	No. examined
Mammals		
Bontebok	*Damaliscus pygargus dorcas*	34
Grey rhebok	*Pelea capreolus*	37
Cape gerbil	*Tatera afra*	1
Four-striped grass mouse	*Rhabdomys pumilio*	25
Scrub hare	*Lepus saxatilis*	11
Birds		
Cape francolin	*Francolinus capensis*	7
Greywing francolin	*Francolinus africanus*	7
Helmeted guineafowl	*Numida meleagris*	4
Reptiles		
Leopard tortoise	*Geochelone pardalis*	9

shot while the rodents were either shot or were trapped and then killed. The tortoises were examined alive.

Parasite recovery

The ticks on the antelopes were collected, identified and counted as described by Horak, Boomker, Spickett & De Vos (1992); those on the rodents and hares as described by Horak *et al.* (1986b); and those on the birds as described by Horak & Williams (1986). All ticks visible on the tortoises were removed with the aid of forceps and placed in 70% ethyl alcohol for later identification and counting. The length of the idiosoma of all engorging female ticks was measured to ascertain how many would have been likely to detach within the next 24 h.

Bot fly larvae were collected from the nasal passages and paranasal sinuses, the eyes, heart and the skin and subcutaneous tissue as described by Malan, Reinecke & Scialdo (1981), Horak, Brown, Boomker, De Vos & Van Zyl (1982) and Horak *et al.* (1986b).

RESULTS AND DISCUSSION

Ixodid ticks

Eleven species of ticks were recovered. Large numbers of four of them were collected and are listed in Table 2. The ticks collected in relatively small numbers or only from a few host species are listed in Table 3.

Amblyomma marmoreum

This tick was present on seven of the nine host species examined. The leopard tortoises were infested with all stages of development and the other animals mainly with larvae. Tortoises are the preferred hosts of the adults (Norval 1975). The immature stages, and particularly the larvae, will infest a large variety of reptiles, mammals and birds (Norval 1975; Horak, MacIvor, Petney & De Vos 1987a). As in the case of *Amblyomma hebraeum* the immature stages do not favour the four-striped grass mouse (Howell, Petney & Horak 1989), or probably any other rodent species, as hosts.

Boophilus sp.

Although no specific identification of the larvae recovered could be made both *Boophilus decoloratus* and *Boophilus microplus* have been collected from a grey rhebok just outside the park (Horak *et al.* 1986b). Infestations of these ticks are maintained by domestic cattle on the farms adjoining the park.

Haemaphysalis aciculifer

Both immature and adult stages were collected. Although this tick is widely distributed, particularly in the eastern regions of South Africa, where its presence is associated with bush and scrub, it is never encountered in large numbers (Walker 1991). The preferred hosts of the adults are various small and large wild bovids while the immatures feed on rodents and hares as well as on other small mammals and carnivores (Hoogstraal & El Kammah 1972; Walker 1991). Cape francolin also appear to be good hosts of the immature stages as nearly all were infested in the present study.

Haemaphysalis leachi

Adult ticks prefer domestic dogs and the larger wild carnivores while the immature stages can be found on these animals, hares and rodents (Norval 1984; Horak, Jacot Guillarmod, Moolman & De Vos 1987b; Fourie, Horak & Van den Heever 1992; Horak, Spickett, Braack & Penzhorn 1993). The source of infestation in the Bontebok Park is probably caracal (*Caracal caracal*) and feral domestic cats as well as domestic dogs which occasionally gain entrance.

TABLE 2 Host records of the more abundant ixodid tick species in the Bontebok National Park

Tick and host species	No. of hosts examined	No. infested	Total numbers of ticks collected				
			Larvae	Nymphs	Males	Females	Total
Amblyomma marmoreum							
Bontebok	34	11	70	0	0	0	70
Grey rhebok	37	11	96	0	0	0	96
Scrub hare	11	3	12	2	0	0	14
Cape francolin	7	3	15	1	0	0	16
Greywing francolin	7	4	129	0	0	0	129
Helmeted guineafowl	4	2	9	1	0	0	10
Leopard tortoise	9	7	7	5	77	19	108
Ixodes sp. (near *I. pilosus*)							
Bontebok	34	16	92	21	2	6	121
Grey rhebok	37	28	888	90	18	83 (11)	1 079
Four-striped grass mouse	25	2	1	1	0	0	2
Scrub hare	11	6	24	3	1	8	36
Rhipicephalus glabroscutatum							
Bontebok	34	29	2 408	358	20	27 (5)	2 813
Grey rhebok	37	27	828	80	26	15	949
Scrub hare	11	4	6	2	0	0	8
Rhipicephalus nitens							
Bontebok	34	34	9 110	122	407	469 (34)	10 108
Grey rhebok	37	35	3 306	29	250	357 (73)	3 942
Scrub hare	11	11	292	176	69	54 (14)	591
Helmeted guineafowl	4	1	1	0	0	0	1

( ) = number of engorging female ticks that could detach within the next 24 h

Hyalomma truncatum

All stages of development were recovered. Adult ticks prefer large herbivores (Norval 1982; Horak, Fourie, Novellie & Williams 1991b) and in the Bontebok Park the adults may be maintained by the Cape mountain zebras (*Equus zebra zebra*) introduced in 1988 and red hartebeest (*Alcelaphus buselaphus caama*). Leopard tortoises, which abound in the park, probably also harbour some adult ticks (Hoogstraal 1956; Table 3). Scrub hares and various rodents are the preferred hosts of the immature stages (Rechav, Zeederberg & Zeller 1987; Horak *et al.* 1991b, 1993). The Western Cape Province south of the Langeberg mountain range does not appear to be a particularly good habitat for this tick, hence the relatively small numbers collected.

Ixodes sp. (near *I. pilosus*)

This tick has been described by McKay (1994) as the "hairless palp" species within the *I. pilosus* group whose distribution is restricted to the coastal forests and coastal fynbos of the eastern and southern Cape. Grey rhebok appear to be its preferred host. This assumption, however, may be partially related to the habitat preferences of both the antelope and the tick. The grey rhebok frequent the gravel terraces and low hills within the park and the tick probably also prefers this habitat. *Ixodes rubicundus*, which is present in the Karoo less than 100 km to the north of the park, is more abundant on hill and mountain slopes than on open plains (Stampa 1959). All stages of development of the *Ixodes* sp. (near *I. pilosus*) were collected also from bontebok and from scrub hares. Females considerably outnumbered males on all hosts infested with adult ticks. As with other species in this genus copulation probably takes place off the host thus accounting for the small number of parasitic males collected (Fourie & Horak 1994).

Rhipicephalus evertsi evertsi

Both the immature and adult stages of development of this two-host tick prefer zebras as hosts (Hoogstraal 1956; Norval 1981; Horak *et al.* 1991b). The population in the park is probably now sustained by the mountain zebras, while the antelope and scrub hares serve as additional hosts for the immature stages.

Rhipicephalus gertrudae

Adults have previously been collected from bontebok and grey rhebok in the park (Horak *et al.* 1986b). The mountain zebras now in the park are also good hosts of the adults (Walker 1991). The latter author suggested

TABLE 3 Host records of the less abundant ixodid tick species in the Bontebok National Park

Tick and host species	No. of hosts examined	No. infested	Total numbers of ticks collected				
			Larvae	Nymphs	Males	Females	Total
Boophilus sp.							
Bontebok	34	1	4	0	0	0	4
Scrub hare	11	2	9	0	0	0	9
Haemaphysalis aciculifer							
Bontebok	34	2	4	0	0	2	6
Grey rhebok	37	2	0	0	0	3 (3)	3
Four-striped grass mouse	25	7	6	5	0	0	11
Cape francolin	7	6	11	7	0	0	18
Haemaphysalis leachi							
Four-striped grass mouse	25	4	83	2	0	0	85
Scrub hare	11	1	7	1	0	0	8
Hyalomma truncatum							
Bontebok	34	1	0	2	0	0	2
Cape gerbil	1	1	1	2	0	0	3
Four-striped grass mouse	25	2	0	4	0	0	4
Scrub hare	11	5	84	23	0	0	107
Leopard tortoise	9	2	0	0	0	2	2
Rhipicephalus evertsi evertsi							
Bontebok	34	5	8	28	0	0	36
Grey rhebok	37	4	11	24	2	1	38
Scrub hare	11	3	7	19	0	0	26
Rhipicephalus gertrudae							
Four-striped grass mouse	25	17	45	28	0	0	73
Scrub hare	11	1	0	3	0	0	3
Cape francolin	7	1	1	0	0	0	1
Helmeted guineafowl	4	1	1	0	0	0	1
Rhipicephalus lounsburyi							
Four-striped grass mouse	25	1	0	1	0	0	1

( ) = number of engorging female ticks that could detach within the next 24 h

that when the hosts of the immature stages were discovered they were likely to be small mammals, probably rodents. This supposition has been confirmed with the collection of larvae and nymphs from Namaqua rock mice (*Aethomys namaquensis*) in the Free State (Fourie *et al.* 1992), and from four-striped grass mice in the present study. The single larva collected in each case from a francolin and from a guineafowl must be regarded as accidental infestations.

Rhipicephalus glabroscutatum

All stages of development were present on the bontebok and grey rhebok. Both adult and immature ticks attach to the lower legs and around the hooves of wild and domestic ruminants and equids (Horak & Knight 1986; Horak, Knight & De Vos 1986a; Horak *et al.* 1991b). Although few ticks were found on scrub hares in the present study, they can be good hosts of the immature stages (Horak & Fourie 1991; Horak *et al.* 1991b).

The life cycle of *R. glabroscutatum* takes a year to complete. Adults are most abundant from July or August to January or February (Horak *et al.* 1986b; MacIvor & Horak 1987) and immatures from February or March to August or September (Horak *et al.* 1986b, 1991b; Horak & Fourie 1991). In the present study a considerably larger number of larvae than nymphs of this two-host tick were collected. This reflects the fact that all the animals were examined during February, at the very commencement of immature activity and consequently few larvae had probably as yet moulted to nymphs.

Rhipicephalus lounsburyi

Adults attach around the feet and hooves of several wild ruminants and of sheep (Walker 1990). The collection of a single nymph from a four-striped grass mouse in the present study is the first record of a host for the immature stages. Adults were previously recorded as *Rhipicephalus* sp. from bontebok and grey rhebok in the park (Horak *et al.* 1986b).

Rhipicephalus nitens

The distribution of this tick is associated with Cape shrubland vegetation (fynbos) in a coastal strip from Cape Town to approximately 60 km west of Port Elizabeth (Walker 1991). It is a three-host species and all stages of development were present on bontebok, grey rhebok and scrub hares. The adults are most abundant from November to February, larvae from February to June and nymphs from June to October (Horak *et al.* 1986b; Horak, Williams & Van Schalkwyk 1991a). These authors remarked that female ticks usually outnumbered males late in the season of adult activity. This trend is discernible in the present study.

The biology of *R. nitens* differs from those of *Rhipicephalus appendiculatus* and *Rhipicephalus zambeziensis*, two ticks that are morphologically similar to it and which also occur in South Africa. The adults of *R. nitens* are most abundant during the hot fairly dry summer and the immature stages during the cool wet winter of the Western Cape Province, and all stages of development are found on antelopes as well as on scrub hares (Horak *et al.* 1986b). The other two ticks occur in the North-West, Northern and Mpumalanga Provinces with *R. appendiculatus* also being present in KwaZulu-Natal and the Eastern Cape Province (Howell, Walker & Nevill 1978; Norval, Walker & Colborne 1982). Their adults are most abundant during the hot wet summer and cooler dry winter months characteristic of their habitats, and all stages of development are found on antelopes, while scrub hares harbour only the immature stages (Horak & Fourie 1991; Horak *et al.* 1992, 1993).

Bot fly larvae

The numbers of bot fly larvae collected from the bontebok and grey rhebok are summarized in Table 4.

Oestrus ovis

The larvae of this fly parasitize domestic sheep and goats and have also been collected from some wild sheep (*Ovis* sp.) and goats (*Capra* sp.) (Zumpt 1965). No wild bovids in Africa south of the Sahara have been found to serve as suitable hosts for the larvae (Zumpt 1965). Although seven grey rhebok in the present study were infested, the fly was apparently unable to complete its life cycle in these animals as all third stage larvae collected were dead. The reason for this failure is possibly twofold. Firstly in sheep and goats the development of second and third stage larvae takes place within the protected environment of the frontal sinuses (Horak 1977). In grey rhebok, which appear to have no frontal sinus cavities, this development has to take place in the more exposed nasal passages. Secondly some of the larvae enter the large maxillary sinuses of the grey rhebok and develop there to mature third stage larvae. These large larvae are, however, unable to leave these sinuses because of the narrowness of the openings and consequently die. The infestation in the park is maintained by sheep on the surrounding farms.

Gedoelstia sp.

No specific identification could be made but the spinulation and the shape of the post-anal bulge of the third stage larvae collected from the bontebok lie

TABLE 4 Host records of oestrid fly larvae collected in the Bontebok National Park

Fly and host species	No. of hosts examined	No. infested	Total numbers of larvae collected			
			1st stage	2nd stage	3rd stage	Total
Oestrus ovis						
Grey rhebok	37	7	2	5	14 (14)	21 (14)
Gedoelstia sp.						
Bontebok	34	34	1 464	765	1 093	3 322
Grey rhebok	37	1	2	0	0	2
Strobiloestrus sp.						
Bontebok	34	4	0	7 (5)	0	7 (5)
Grey rhebok	37	35	0	607	0	607

( ) = dead larvae included in totals

between those of *Gedoelstia cristata* and *Gedoelstia hässleri*. These larvae may well belong to a hitherto undescribed species of oestrid fly.

All the bontebok were infested. Twenty-two first stage larvae were recovered from the corneas of five animals, 639 first stage larvae from the auricle and the ventricle of the right heart and the commencement of the pulmonary artery of 23 animals, and two from the lungs of a single antelope. A slight corneal opacity was evident on an eye of one animal. The first stage larvae migrate via the eyes, the vascular system, the heart, the lungs and the trachea to reach the paranasal sinus cavities of the bontebok. The fairly large proportion of first stage larvae recovered from the chambers of the right heart implies that they may accumulate here before completing their migration. In blue wildebeest (*Connochaetes taurinus*) first stage *Gedoelstia* spp. larvae appear to accumulate on the dura mater before migrating to the paranasal sinus cavities (Horak, De Vos & Brown 1983).

Basson (1962, 1966) has described the pathology of infestation in natural and abnormal hosts. First stage *Gedoelstia* spp. larvae cause little macroscopically-visible damage to the eyes of their natural hosts, which include the bontebok (Basson, 1966). Hence the virtual absence of lesions in this animal. Grey rhebok are abnormal or accidental hosts of these fly larvae and corneal lesions were present in 11 animals, with both eyes of two rhebok being affected. The lesions varied from slight opacities to purrulent conjunctivitis, and in one case enucleation. Two first stage larvae were collected from the cornea of one animal. Basson (1962) also noted that the life cycle cannot progress beyond the first larval stage in abnormal hosts and no second or third stage larvae were collected from the grey rhebok.

Strobiloestrus sp.

The larvae collected from the grey rhebok and from the bontebok are probably those of *Strobiloestrus clarkii* (Zumpt 1965). As no mature third stage larvae were present we were unable to rear flies and confirm this.

All but two of the grey rhebok were infested with second instar larvae, the largest number harboured by a single animal comprising 130 larvae. The life cycle of this fly takes a year to complete, and only second stage larvae are present during February, the month in which all the animals were examined (Horak *et al.* 1986b). Grey rhebok are the normal hosts as virtually all were infested and third stage larvae, which were nearly mature, have previously been collected from these animals (Horak *et al.* 1986b). The small number of bontebok infested and the large proportion of dead larvae collected from them indicate that they are abnormal hosts and the infestations accidental. Accidental infestations have also been recorded in domestic cattle and in Merino sheep (Horak & Boomker 1981; Brain, Van der Merwe & Horak 1983).

ACKNOWLEDGEMENTS

We wish to thank the South African National Parks for placing the animals and the facilities in the Bontebok National Park at our disposal. We gratefully acknowledge the assistance of the successive park wardens Messrs E. Fourie, B. de Klerk, A. Hofmeyr and O. von Kaschke and their staff as well as that of Dr J.P. Louw with the processing of the necropsies. Mr E.J. Williams and Miss Louise Horak assisted with the collection of ticks from the processed material, and Dr I.J. McKay identified the *Ixodes* species.

The research was funded by the University of Pretoria, Rhodes University and the Foundation for Research Development.

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Onderstepoort Journal of Veterinary Research, 70:131–163 (2003)

Parasites of domestic and wild animals in South Africa. XLI. Arthropod parasites of impalas, *Aepyceros melampus*, in the Kruger National Park

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ABSTRACT

HORAK, I.G., GALLIVAN, G.J., BRAACK, L.E.O., BOOMKER, J. & DE VOS, V. 2003. Parasites of domestic and wild animals in South Africa. XLI. Arthropod parasites of impalas, *Aepyceros melampus*, in the Kruger National Park. *Onderstepoort Journal of Veterinary Research*, 70:131–163

Ectoparasites were collected from impalas, *Aepyceros melampus*, at four localities within the Kruger National Park, namely Skukuza, in the Biyamiti region, Crocodile Bridge and Pafuri. Animals were also examined at Skukuza during a severe drought and at Skukuza and Pafuri towards the end of a second drought. Parasite burdens were analysed in relation to locality, sex, age class, month and drought.

The impalas were infested with 13 ixodid ticks species, including two that were identified only to genus level. Except for four animals at Pafuri, all were infested with *Amblyomma hebraeum*. The highest intensity of infestation with larvae of this tick occurred from April to June and during November and December at Skukuza and in the Biyamiti region. Infestation with nymphs was highest during late winter. All animals were infested with *Boophilus decoloratus*, and the intensity of infestation was highest during spring. The intensity of infestation with *Rhipicephalus appendiculatus* was highest at Crocodile Bridge and at Pafuri, and that of *Rhipicephalus zambeziensis* at Skukuza. With both the latter species the intensity of infestation of larvae was highest from April to August, of nymphs from July to September or October and of adults during February and March. *Rhipicephalus kochi* was present only at Pafuri.

The impalas also harboured five louse species and two species of hippoboscid flies. The intensity of infestation with lice tended to be greater during late winter and spring than during other seasons and greater on lambs than on yearlings on which it was greater than on adult animals.

Keywords: *Aepyceros melampus*, drought, hippoboscid flies, impalas, intensity of infestation, ixodid ticks, Kruger National Park, lice, prevalence, seasonality

INTRODUCTION

Impalas, *Aepyceros melampus*, are widely distributed in the eastern woodland regions of Africa, from northern Kenya south to northern KwaZulu-Natal, South Africa, with their southern distribution extending north-westward to south-eastern Angola and northern Namibia. They prefer light, open woodland communities and generally avoid open grassland unless it abuts on woodland (Skinner & Smithers 1990). Impalas are classified as intermediate mixed feeders as they both graze and browse (Skinner &

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Accepted for publication 3 March 2003—Editor

Smithers 1990), and within their range they are often the most numerous medium-sized antelopes. In South Africa they are present in national, provincial and privately owned nature reserves as well as on many mixed cattle and wildlife ranches.

With the possible exception of African buffaloes, *Syncerus caffer*, more surveys have been conducted on the arthropods infesting impalas than on those of any other wild African mammal. The ixodid tick species infesting impalas in sub-Saharan Africa have been listed by Theiler (1962); those in Kenya by Walker (1974); in Tanzania by Yeoman & Walker (1967); in Zambia by MacLeod (1970), Colbo (1973) and MacLeod & Mwanaumo (1978); in Botswana by Paine (1982); in Mozambique by Santos Dias (1993); in Swaziland by Gallivan & Surgeoner (1995); and in South Africa by Meeser (1952) and Baker & Keep (1970). Total, or calculated total tick burdens have been determined on these animals in Zambia (Zieger, Horak, Cauldwell, Uys & Bothma 1998), Zimbabwe (Colborne 1989; Mooring & McKenzie 1995; Mooring & Mazhowu 1995), Swaziland (Gallivan, Culverwell, Girdwood & Surgeoner 1995) and in South Africa in Limpopo Province (Horak 1982; Matthee, Meltzer & Horak 1997), Mpumalanga Province (Horak, Boomker, Kingsley & De Vos 1983c; Horak, Fourie & Van Zyl 1995c), North West Province (Van Dyk & McKenzie 1992) and KwaZulu-Natal (Horak, Keep, Flamand & Boomker 1988a). The louse species that infest impalas are listed by Ledger (1980), and their total louse burdens have been determined by Horak (1982), Horak *et al.* (1983c), Van Dyk & McKenzie (1992) and Matthee, Horak & Meltzer (1998). The flies recorded on these animals are listed by Haeselbarth, Segerman & Zumpt (1966).

The tick species infesting impalas are similar to those found on domestic cattle farmed in the same regions (Yeoman & Walker 1967; Walker 1974; Horak 1982; Colborne 1989), and those on sympatric antelope species (Gallivan & Surgeoner 1995; Horak 1998). Impalas appear to harbour larger tick infestations than other medium-sized antelope species (Gallivan & Horak 1997; Horak 1998), and may thus serve as an important reservoir of tick infestation on mixed cattle and wildlife farms (Horak 1982; Colborne 1989), and on game ranches or wildlife reserves, on which they are frequently the most numerous antelope species (Gallivan & Surgeoner 1995; Zieger *et al.* 1998). As lice are obligate permanent parasites, and those infesting impalas are host-specific, there is little possibility of cross-infestation with these parasites occurring with sympatric wild or domestic animals.

In this paper we compare the tick, louse and hippoboscid fly burdens of impalas examined in four landscape zones within the Kruger National Park (KNP). We also examine the seasonal intensity of infestation, and the relationships between infestation with the most abundant species of ectoparasites and host age and sex class.

MATERIALS AND METHODS

Survey animals

A total of 229 impalas were examined in several surveys in the Kruger National Park. Each animal was killed during the morning by a single shot in the neck from a small or large calibre rifle. The locations, seasons and age and sex classes of the animals are summarised in Table 1. Because parturition in these animals in southern Africa is generally confined to the months November to January (Skinner & Smithers 1990), it is possible to visually age impalas fairly accurately until the age of 2 years, particularly the males because of the age-associated changes in the shape of their horns. It is more difficult with the females that are hornless.

Parasite recovery

The impalas were processed for the recovery of arthropod parasites as described by Horak, Boomker, Spickett & De Vos (1992) for greater kudus, *Tragelaphus strepsiceros*. Ticks, lice and hippoboscid flies were collected from the processed material under stereoscopic microscopes, and identified and counted under the same microscopes. We estimate that the idiosoma of female *Boophilus decoloratus* would reach a minimum length of 4.0 mm 24 h before detachment, and the length of the idiosoma of engorging female ticks of this species was measured.

Survey localities

Skukuza (24°58'S, 31°36'E; Alt. 262 m)

Skukuza is a tourist rest camp, and is also the headquarters of the South African National Parks Kruger Park Management and Research divisions, situated in the south-western region of the KNP in a landscape zone described as Thickets of the Sabie and Crocodile Rivers (Gertenbach 1983) of which the vegetation is classified as Lowveld (Acocks 1988). The impalas examined in this region were shot within a 25 km radius of Skukuza. Three to seven animals were shot each month from January 1980 to January 1981, and always included a lamb (< 12 months of age), a yearling male (12– 23 months) and an adult (> 24 months). From February to May 1981 two to four animals were shot each month, always including an adult male and an adult female.

During the drought that occurred in 1982/83 a large number of impalas died from starvation in October and November 1982. Ten animals, considered terminally affected by the drought, were shot for survey purposes during these months. At the same time 14 apparently healthy animals were shot for comparison at the same locality. A severe drought occurred during 1991/92, and in March 1992 six 15-month-old impala males were shot and examined for parasites. Three yearling males were shot at the same locality and examined every month thereafter until April 1993.

Biyamiti region (25°06'–25°28'S, 31°25'–31°39'E; Alt. 200–350 m)

This survey site is located in the central southern region of the KNP in a landscape zone described as Mixed Bushwillow Woodlands (Gertenbach 1983) of which the vegetation is classified as Lowveld (Acocks 1988). It extended from north of the Biyamiti River to north of the Malelane entrance gate to the KNP. Each month from January 1980 to May 1981 two to six impalas, generally of the same ages and sexes as those shot at Skukuza, were shot in this locality and examined.

Crocodile Bridge (25°22'S, 31°54'E; Alt. 217 m)

Crocodile Bridge is a tourist rest camp close to the south-eastern border of the KNP. The vegetation is classified as Lowveld by Acocks (1988) and the landscape zone described as Marula/Knobthorn (*Sclerocarya caffra/Acacia nigrescens*) Savanna (Gertenbach 1983). Each month from January 1980 to January 1981 a single adult male impala was shot in the Crocodile Bridge region and examined for parasites.

Pafuri (23°27'S, 31°19'E; Alt. 305 m)

Pafuri is located in the far north-east of the KNP. The vegetation here is classified as Mixed Bushveld (Acocks 1988) and the landscape described as Limpopo/Levubu Floodplains by Gertenbach (1983). During July 1980, a lamb, a yearling, an adult male, and an adult female impala were shot and examined. From March 1992 to April 1993, three yearling males were shot and examined at 2–3 month intervals.

Climate

Monthly mean minimum and maximum atmospheric temperatures and total monthly rainfall were recorded at Skukuza, and are presented graphically in Fig. 1 for the periods 1979–1983 and 1990–1993.

Statistical analysis

Factors of interest in the analysis of the data were the effects of the location, season, age class, sex of the adult impalas, differences between years, and drought. However, because the collections were independent and factors were not balanced across studies it was not possible to analyse the data in a single multivariate analysis. Therefore, the data were subdivided and analysed in the following groups:

- Skukuza versus the Biyamiti region in 1980/81
- Skukuza, the Biyamiti region and Crocodile Bridge in 1980/81 (adult males only)
- Skukuza 1980/81 versus 1992/93
- Skukuza versus Pafuri in 1992/93
- Skukuza, Biyamiti and Pafuri in July 1980
- The 1982 drought

The factors analysed in each grouping are presented in Table 1. Differences in location and season were assessed by comparisons of the results of the individual analyses.

Most analyses compared both the prevalence and the intensity of infestation. Differences in prevalence were analysed using contingency tables with a x^2. For differences in the intensity of infestation, the parasite count data were logarithmically transformed to reduce the inequality of variance created by overdispersion (Petney, Van Ark & Spickett 1990). The data were then analysed using analysis of variance. In all of the analyses, factors were restricted to ensure equal balance among the groups. When factors were significant, a t-test was used to test between two groups and a Student-Newman-Keuls multiple range test was used to test among multiple groups. Because the 1980/81 and 1992/93 collections extended over 2 consecutive years and there was a potential for year-to-year variation, month was converted to a continuous variable starting in January of the first year (1980 or 1992). Animals less than 3 years old were aged to month; i.e., they were classed as lambs (0–11 months), yearlings (12–23 months) or adults (older than 24 months) in the analyses. In 1992/93, three to six yearling males per month were collected at Skukuza, and three

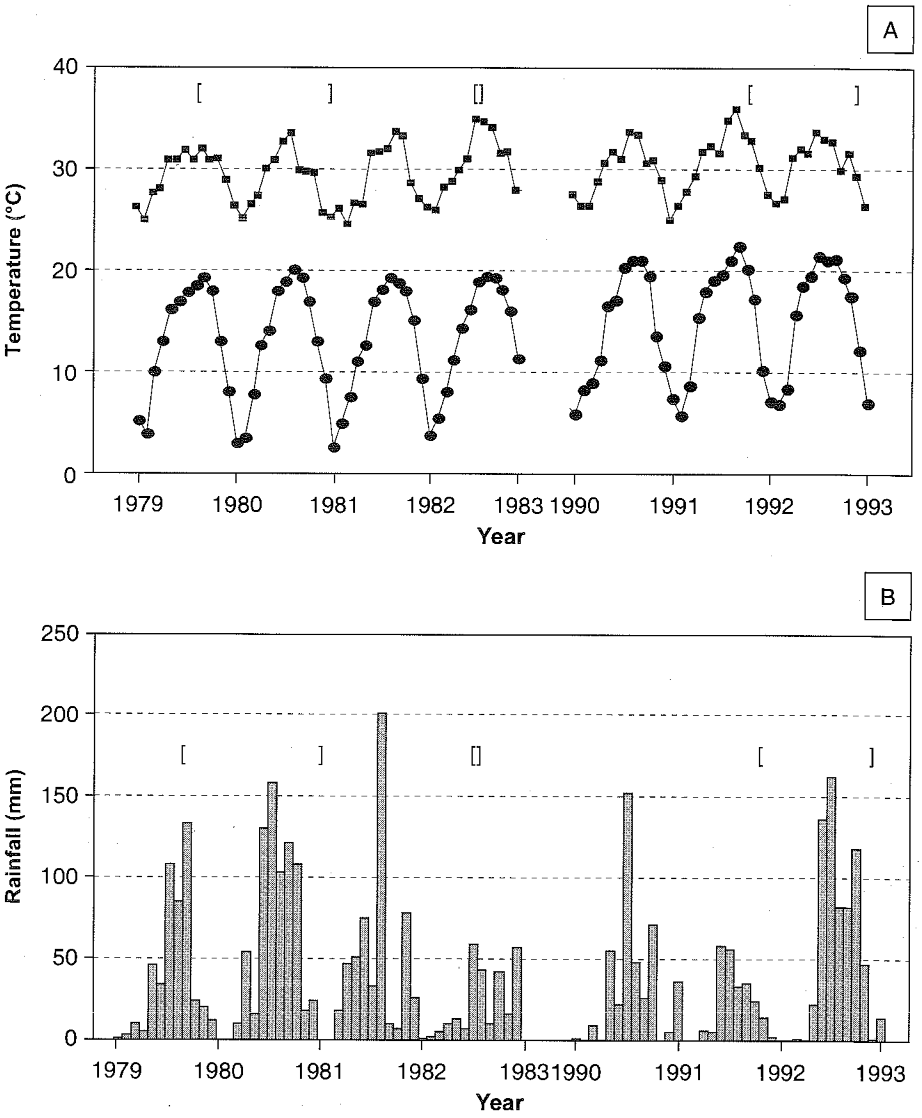

FIG. 1 [A] Average monthly minimum and maximum temperatures (°C) and [B] total monthly rainfall (mm) at Skukuza (1979–1983; and 1990–1993). Periods within brackets represent the survey periods

were collected at 2–3 month intervals at Pafuri. However, only one yearling was collected per month at Skukuza in 1980/81. To compare the parasite burdens at Skukuza in 1980/81 and 1992/93, the yearlings in 1992/93 were compared to the yearlings and adults in 1980/81 for the ticks, and to the lambs and yearlings for the lice. The groupings for 1980/81 were based on the results of the analysis for age effects. Because the 1982 drought potentially affected the parasite burdens of both the "terminal" and apparently healthy impalas, their parasite burdens were also compared to those from impalas collected during the same time period at Skukuza in 1980.

RESULTS AND DISCUSSION

IXODID TICKS

Total tick burdens

The impalas were infested with 13 species of ixodid ticks, of which 11 were identified to species level and two to genus level. Six species, *Amblyomma hebraeum, Amblyomma marmoreum, B. decoloratus, Rhipicephalus appendiculatus, Rhipicephalus evertsi evertsi* and *Rhipicephalus zambeziensis* were commonly collected at all locations, while *Rhipicephalus kochi* was only common at Pafuri (Table 2). The other species, *Amblyomma tholloni,*

TABLE 1 Groups, factors and ANOVA procedures used in the statistical analysis of the arthropod parasite burdens of impalas in the Kruger National Park

Group	Factors assessed	Statistical procedure	Comments
Skukuza vs Biyamiti	Location, month, age, sex	Three-factor ANOVAs: location, month and age; and location, month and sex	Location, month, age: month restricted to Jan 1980 to Jan 1981 Location, month, sex: adults only, month restricted to Mar 1980 to Apr 1981 (no adult females in Jan and Feb 1980)
Skukuza, Biyamiti and Crocodile Bridge	Location, month	Two-factor ANOVA	Adult males only, month restricted to Jan 1980 to Jan 1981
Skukuza 1980/81 vs 1992/93	Year, month	Two-factor ANOVA	Yearlings only in 1992/93 compared to yearlings and adults in 1980/81 for ticks; and to lambs and yearlings in 1980/81 for lice, months restricted to March 1980/92 to February 1981/93 (lice) or April 1981/93 (ticks)
Skukuza vs Pafuri 1992/93	Location, month	Two-factor ANOVA	Yearlings only, months matched to collections at Pafuri
Skukuza, Biyamiti and Pafuri	Location	One-factor ANOVA	July 1980 only, lamb, yearling and adults at each location
Skukuza 1982 drought	Group	One-factor ANOVA	“Terminal” vs “apparently healthy” impalas in 1982 compared to impalas collected in 1980 in same time period

TABLE 2 Proportional intensity of infestation of the major tick and louse species on impalas examined over a period of 12 months or more at four localities in the Kruger National Park

Arthropod species	Proportional intensity of infestation (%)				
	Skukuza (1980/81) (*n* = 63)	Skukuza (1992/93) (*n* = 45)	Biyamiti (1980/81) (*n* = 60)	Crocodile Bridge (1980/81) (*n* = 12)	Pafuri (1992/93) (*n* = 21)
Ticks					
Amblyomma hebraeum	24.07	25.05	10.56	21.49	6.31
Amblyomma marmoreum	0.60	1.38	0.05	0.14	0.07
Boophilus decoloratus	56.85	45.80	70.13	47.74	46.75
Rhipicephalus appendiculatus	2.13	0.64	5.37	24.03	15.82
Rhipicephalus evertsi evertsi	3.25	2.17	10.49	3.84	5.09
Rhipicephalus kochi	0.00	0.00	0.00	0.00	20.57
Rhipicephalus zambeziensis	13.08	24.95	3.39	2.75	5.34
Lice					
Damalinia aepycerus	18.57	22.75	21.02	10.05	18.93
Damalinia elongata	61.94	54.83	6.96	46.89	0.04
Linognathus aepycerus	11.35	18.14	34.53	42.82	65.20
Linognathus nevilli	6.58	3.17	33.68	0.24	14.33

n = Number of impalas examined

Haemaphysalis aciculifer, *Hyalomma truncatum*, *Ixodes* sp., *Rhipicephalus simus* and the *Rhipicephalus pravus* group were incidental or sporadic infestations (Tables 3–10).

The tick species infesting the impalas were similar to those collected from sympatric antelope species that had previously been examined in the KNP (Horak, Potgieter, Walker, De Vos & Boomker 1983a; Horak, De Vos & Brown 1983b; Horak *et al.* 1992; Horak 1998). Impalas appear to harbour disproportionately large tick burdens for their size (Gallivan & Horak 1997; Horak 1998), and the mean tick burden of the animals examined in the Biyamiti region was similar to the mean burden of greater kudus examined there 2 years later (Horak *et al.* 1992). However, a greater proportion of the ticks on the kudus consisted of adults, which supports the suggestion that larger ungulates are more important hosts for adult ticks (MacLeod 1970; Horak 1982). The tick burdens of the impalas would conceivably have been considerably larger if self-grooming, and probably also allogrooming, which are effective in removing ticks (A.A. McKenzie, unpublished data, cited by Hart & Hart 1992), are taken into account. Impalas are also one of the few smaller antelope species attended by red-billed oxpeckers, *Buphagus erythrorhynchus* (Stutterheim 1981), and these birds are capable of consuming large numbers of ticks (Bezuidenhout & Stutterheim 1980). In addition the method we used to collect ticks from the impalas was not the most efficient (Van Dyk & McKenzie 1992), but it did provide ticks, lice and flies that could all be identified.

The total tick burdens did not differ significantly among the locations, but there were differences in the prevalence and/or intensity of infestation of some species. These will be discussed in more detail below.

The total tick burden was significantly higher at Skukuza in 1980/81 than in 1992/93 ($P < 0.001$) (Table 11), and was higher at Pafuri in July 1980 than in August 1992 ($P < 0.1$). In contrast to 1992/93, the total tick burden of the impalas examined in 1980 at Skukuza was slightly higher than the burdens of the apparently healthy animals in the 1982 drought. The "terminal" impalas in 1982 had higher total tick burdens than the apparently healthy animals killed

TABLE 3 Arthropod parasites collected during 1980/81 from 63 impalas at Skukuza, Kruger National Park

Arthropod species	Number of arthropods collected				Total	Proportional abundance %	No. of impalas infested
Ixodid ticks	Larvae	Nymphs	Males	Females			
Amblyomma hebraeum	57 227	7 985	52	8	65 272	24.07	63
Amblyomma marmoreum	1 605	21	0	0	1 626	0.60	28
Boophilus decoloratus	88 620	43 029	15 148	7 353 (95)	154 150	56.85	63
Ixodes sp.	0	8	0	0	8	0.003	1
Rhipicephalus appendiculatus	3 298	1 387	737	355	5 777	2.13	53
Rhipicephalus evertsi evertsi	7 328	1 338	109	43	8 818	3.25	61
Rhipicephalus simus	16	0	0	0	16	0.006	1
Rhipicephalus zambeziensis	26 342	7 112	1 415	606	35 475	13.08	60
Lice	Nymphs		Adults				
Damalinia aepycerus	7 448		2 780		10 228	18.57	47
Damalinia elongata	22 188		11 928		34 116	61.94	47
Linognathus aepycerus	3 896		2 356		6 252	11.35	49
Linognathus nevilli	2 440		1 184		3 624	6.58	27
Linognathus sp.	428		428		856	1.55	18
Louse flies	Adults						
Hippobosca fulva	50				50	90.91	19
Lipoptena paradoxa	5				5	9.09	4

( ) = Number of maturing *B. decoloratus* females, i.e. idiosoma > 4.0 mm in length

TABLE 4 Arthropod parasites collected during 1980/81 from 60 impalas in the Biyamiti region, Kruger National Park

Arthropod species	Number of arthropods collected				Total	Proportional abundance %	No. of impalas infested
Ixodid ticks	Larvae	Nymphs	Males	Females			
Amblyomma hebraeum	27 225	3 559	25	4	30 813	10.56	60
Amblyomma marmoreum	159	0	0	0	159	0.05	8
Boophilus decoloratus	126 952	50 692	18 276	8 724 (134)	204 644	70.13	60
Haemaphysalis aciculifer	16	0	0	0	16	0.005	1
Rhipicephalus appendiculatus	9 393	5 892	225	151	15 661	5.37	54
Rhipicephalus evertsi evertsi	26 628	3 865	81	35	30 609	10.49	59
Rhipicephalus simus	0	0	1	0	1	0.0003	1
Rhipicephalus zambeziensis	7 575	1 889	303	123	9 890	3.39	54
Lice	Nymphs		Adults				
Damalinia aepycerus	1 328		944		2 272	21.02	37
Damalinia elongata	340		412		752	6.96	17
Linognathus aepycerus	2 164		1 568		3 732	34.53	37
Linognathus nevilli	2 388		1 252		3 640	33.68	34
Linognathus sp.	240		172		412	3.81	11
Louse flies	Adults						
Hippobosca fulva	117				117	97.50	18
Lipoptena paradoxa	3				3	2.50	1

( ) = Number of maturing *B. decoloratus* females, i.e. idiosoma > 4.0 mm in length

TABLE 5 Arthropod parasites collected during 1992/93 from 45 yearling impala males at Skukuza, Kruger National Park

Arthropod species	Number of arthropods collected				Total	Proportional abundance %	No. of impalas infested
Ixodid ticks	Larvae	Nymphs	Males	Females			
Amblyomma hebraeum	5 076	1 070	8	0	6 154	25.05	45
Amblyomma marmoreum	340	0	0	0	340	1.38	22
Boophilus decoloratus	4 678	3 792	1 619	1 164 (20)	11 253	45.80	45
Hyalomma truncatum	2	0	0	0	2	0.01	1
Rhipicephalus appendiculatus	12	4	96	46	158	0.64	18
Rhipicephalus evertsi evertsi	410	92	20	12	534	2.17	34
Rhipicephalus zambeziensis	3 840	936	942	412	6 130	24.95	40
Lice*	Nymphs		Adults				
Damalinia aepycerus	1 750		1 131		2 881	22.75	41
Damalinia elongata	2 707		4 237		6 944	54.83	29
Linognathus aepycerus	1 195		1 102		2 297	18.14	39
Linognathus nevilli	271		130		401	3.17	18
Linognathus sp.	66		75		141	1.11	16

* = Only 42 animals examined for lice

( ) = Number of maturing *B. decoloratus* females, i.e. idiosoma > 4.0 mm in length

TABLE 6 Arthropod parasites collected during 1980/81 from 12 adult male impalas at Crocodile Bridge, Kruger National Park

Arthropod species	Number of arthropods collected				Total	Proportional abundance %	No. of impalas infested
Ixodid ticks	Larvae	Nymphs	Males	Females			
Amblyomma hebraeum	9 679	1 811	9	2	11 501	21.49	12
Amblyomma marmoreum	77	0	0	0	77	0.14	2
Boophilus decoloratus	11 040	8 260	4 300	1 947 (126)	25 547	47.74	12
Rhipicephalus appendiculatus	10 420	1 888	286	265	12 859	24.03	–
Rhipicephalus evertsi evertsi	1 664	314	61	18	2 057	3.84	12
Rhipicephalus simus	0	0	1	0	1	0.002	1
Rhipicephalus zambeziensis	1 408	48	11	7	1 474	2.75	8
Lice	Nymphs		Adults				
Damalinia aepycerus	96		72		168	10.05	4
Damalinia elongata	552		232		784	46.89	5
Linognathus aepycerus	524		192		716	42.82	6
Linognathus nevilli	4		0		4	0.24	1
Louse flies	Adults						
Hippobosca fulva	4				4	100.00	2

( ) = Number of maturing *B. decoloratus* females, i.e. idiosoma > 4.0 mm in length

TABLE 7 Arthropod parasites collected during the 1982 drought from ten drought-affected "terminal" impalas at Skukuza, Kruger National Park

Arthropod species	Number of arthropods collected				Total	No. of impalas infested
Ixodid ticks	Larvae	Nymphs	Males	Females		
Amblyomma hebraeum	5 715	853	99	49	6 716	10
Amblyomma marmoreum	27	2	0	0	29	4
Boophilus decoloratus	34 964	16 437	8 354	4 967 (60)	64 722	10
Ixodes sp.	1	0	0	0	1	1
Rhipicephalus appendiculatus	56	48	15	21	140	8
Rhipicephalus evertsi evertsi	2 224	264	51	28	2 567	9
Rhipicephalus zambeziensis	80	315	41	48	484	10
Lice	Nymphs		Adults			
Damalinia aepycerus	272		517		789	9
Damalinia elongata	3 896		2 008		5 904	4
Linognathus aepycerus	7 582		8 359		15 941	9
Linognathus nevilli	552		265		817	6
Linognathus sp.	1 264		520		1 784	4
Louse flies	Adults					
Lipoptena paradoxa	4				4	2

( ) = Number of maturing *B. decoloratus* females, i.e. idiosoma > 4.0 mm in length

TABLE 8 Arthropod parasites collected during the 1982 drought from 14 apparently healthy impalas at Skukuza, Kruger National Park

Arthropod species	Number of arthropods collected				Total	No. of impalas infested
Ixodid ticks	Larvae	Nymphs	Males	Females		
Amblyomma hebraeum	11 127	1 160	35	6	12 328	14
Boophilus decoloratus	19 597	16 051	6 307	3 168 (43)	45 123	14
Ixodes sp.	0	17	0	0	17	2
Rhipicephalus appendiculatus	4	120	18	8	150	10
Rhipicephalus evertsi evertsi	1 393	260	16	13	1 682	14
Rhipicephalus zambeziensis	5	180	18	22	225	9
Lice	Nymphs		Adults			
Damalinia aepycerus	233		723		956	14
Damalinia elongata	266		558		824	7
Linognathus aepycerus	1 389		2 282		3 671	13
Linognathus nevilli	48		152		200	5
Linognathus sp.	90		216		306	7
Louse flies	Adults					
Hippobosca fulva	2				2	1
Lipoptena paradoxa	5				5	3

( ) = Number of maturing *B. decoloratus* females i.e. idiosoma > 4.0 mm in length

TABLE 9 Arthropod parasites collected during 1980 from an impala lamb, yearling and adult male, and adult female at Pafuri, Kruger National Park

Arthropod species	Number of arthropods collected				Total	No. of impalas infested
Ixodid ticks	Larvae	Nymphs	Males	Females		
Amblyomma hebraeum	1 105	196	0	0	1 301	4
Amblyomma marmoreum	11	0	0	0	11	1
Boophilus decoloratus	3 252	736	301	82	4 371	4
Rhipicephalus appendiculatus	3 832	2 280	1	1	6 114	4
Rhipicephalus evertsi evertsi	88	40	0	1	129	3
Rhipicephalus kochi	32	80	0	0	112	4
Rhipicephalus pravus group	8	0	0	0	8	1
Rhipicephalus zambeziensis	116	0	0	0	116	3
Lice	Nymphs		Adults			
Damalinia elongata	28		36		64	4
Linognathus aepycerus	16		0		16	1
Linognathus nevilli	432		168		600	4

TABLE 10 Arthropod parasites collected during 1992/93 from 21 yearling impala males at Pafuri, Kruger National Park

Arthropod species	Number of arthropods collected				Total	Proportional abundance %	No. of impalas infested
Ixodid ticks	Larvae	Nymphs	Males	Females			
Amblyomma hebraeum	440	308	4	0	752	6.31	17
Amblyomma marmoreum	8	0	0	0	8	0.07	2
Amblyomma tholloni	0	6	0	0	6	0.05	2
Boophilus decoloratus	1 842	1 982	1 032	712 (52)	5 568	46.75	21
Rhipicephalus appendiculatus	1 076	756	30	22	1 884	15.82	13
Rhipicephalus evertsi evertsi	464	112	28	2	606	5.09	20
Rhipicephalus kochi	1 884	416	118	32	2 450	20.57	17
Rhipicephalus zambeziensis	266	54	190	126	636	5.34	16
Lice	Nymphs		Adults				
Damalinia aepycerus	624		264		888	18.93	15
Damalinia elongata	0		2		2	0.04	1
Linognathus aepycerus	2 072		986		3 058	65.20	19
Linognathus nevilli	482		190		672	14.33	14
Linognathus sp.	40		30		70	1.49	5

( ) = Number of maturing *B. decoloratus* females i.e. idiosoma > 4.0 mm in length

at the same time ($P = 0.065$) (Table 11), but when the 1980 impalas were included, the differences among the groups were marginal ($P = 0.11$).

The apparent differences in the effects of drought on tick burdens may result from differences in the timing of the collections in relation to rainfall. The collections in 1992/93 began in March 1992. They were made in a year of above average rainfall following 2 years of below average rainfall at the end of a dry cycle, with particularly low rainfall during the summer of 1991/92. There was a marked reduction in the number of questing ticks collected by drag-sampling at Skukuza in 1992/93 (Horak, De Vos & Braack 1995b). This probably resulted from a reduction in the number of hosts and a loss of habitat for free-living ticks. Only 1 000 impalas were counted in the 1992 game counts, a quarter of the average count for other years, and there was a decrease in the amount of standing vegetation and loss of the grass mat which provide habitat for the free-living stages of ticks (Horak *et al.* 1995b). The 1982 collections were made in November and early December, at the beginning of the 1982/83 drought. The collections followed an extended period of low rainfall beginning in February 1982. However, this drought occurred at the end of the wet cycle of the 1970s (Whyte & Joubert 1988), and was preceded by 2 years of average to above average rainfall and impala populations (Horak *et al.* 1995b). There were no collections of questing ticks in 1982 but the numbers were probably higher than in 1992. The higher total tick burden on the "terminal" impalas in 1982 is similar to the observation that impalas in poor condition in the spring in the Mlawula-Mbuluzi-Simunye Nature Reserve complex in Swaziland were more heavily infested than those in better condition (Gallivan *et al.* 1995).

The seasonal patterns of infestation were similar in the three southern locations. The total tick burdens of the impalas examined at Skukuza and in the Biyamiti region during 1980/81 were lowest in the summer and highest in the late winter and spring ($P < 0.001$), with a secondary peak in April (Fig. 2). The late winter/spring peak coincides with the hatch and subsequent availability of *B. decoloratus* larvae, and the April peak coincides with the availability of *R. appendiculatus* and *R. zambeziensis* larvae. There was a significant month x location interaction ($P = 0.002$) caused by higher burdens at Skukuza from January to June 1980, and higher burdens in the Biyamiti region from July 1980 to January 1981. The higher burdens at Skukuza were caused by the higher intensity of infestation of *R. zambeziensis* larvae, while the higher burdens in the Biyamiti region were caused by the higher intensity of infestation of *B. decoloratus*.

TABLE 11 Mean intensities of infestations of arthropods on impalas during the 1982 and 1992 droughts in the Kruger National Park compared to animals examined during 1980/81

Arthropod species	Stage of development	1982			1992	
		"Terminal" (*n* = 10)	Healthy (*n* = 14)	1980 (*n* = 14)	1980/81 (*n* = 41)	1992/93 (*n* = 45)
Ixodid ticks						
Amblyomma hebraeum	Larvae	571.5	794.8	1 023.5	892.6	112.8
	Nymphs	85.3	82.9	138.4	138.3	23.8
	Adults	14.8	2.9	0.8	1.1	0.2
Amblyomma marmoreum	Larvae	2.7	0	13.6	29.9	7.6
Boophilus decoloratus	All	6 472.2	3 223.1	3 161.1	2 641.6	250.1
Rhipicephalus appendiculatus	Larvae	5.6	0.3	5.7	40.1	0.3
	Nymphs	4.8	8.6	1.1	23.1	0.1
	Adults	3.6	1.9	0.8	18.8	3.1
Rhipicephalus evertsi evertsi	Immatures	248.8	118.1	155.4	141.9	11.2
	Adults	7.9	2.1	3.0	2.8	0.7
Rhipicephalus zambeziensis	Larvae	8.0	0.4	0.0	342.5	85.3
	Nymphs	31.5	12.9	44.0	90.2	20.8
	Adults	8.9	2.9	2.1	37.3	30.1
Total ixodid ticks		7 492.7	4 251.8	4 549.6	4 400.9	546.0
Lice					*	*
Damalinia aepycerus	Nymphs, adults	78.9	68.3	108.0	249.3	70.2
Damalinia elongata	Nymphs, adults	590.4	58.9	207.4	1 029.3	175.0
Linognathus aepycerus	Nymphs, adults	1 594.1	262.2	89.7	97.5	58.5
Linognathus nevilli	Nymphs, adults	81.7	14.3	46.9	77.7	10.1
Linognathus sp.	Nymphs, adults	178.4	21.9	22.3	23.2	3.3
Total lice		2 523.5	425.5	474.3	1 477.1	317.2

* For lice *n* = 21 in 1980/81 and 39 in 1992/93

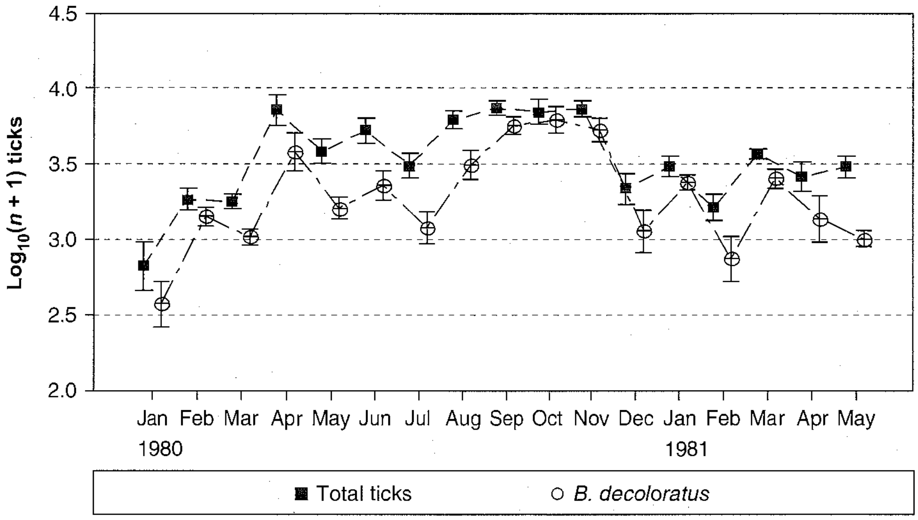

FIG. 2

Seasonal pattern of the total tick burden and intensity of infestation of all life stages of *Boophilus decoloratus* (x ± 1SE) on impalas at Skukuza and in the Biyamiti region in 1980/81. No lambs were collected after January 1981 and no yearlings after February 1981. The monthly sample at each locality ranged from two to six or seven impalas

The seasonal pattern at Skukuza was similar in 1980/81 and 1992/93. However, there was a significant month x location interaction ($P = 0.004$) between Skukuza and Pafuri in 1992/93. Burdens were significantly higher ($P < 0.05$) at Skukuza in the spring and summer, and tended to be higher at Pafuri in the autumn and winter, although the latter differences were not statistically significant ($P > 0.05$). The higher tick burdens at Pafuri corresponded to periods with the highest intensity of infestation of *B. decoloratus* and *R. kochi* at this location, and the higher burdens at Skukuza corresponded with the peak activity period of *B. decoloratus* at the southern locations in the KNP.

The total tick burdens during 1980/81 at Skukuza and in the Biyamiti region were significantly lower on lambs than on yearlings and adults ($P = 0.004$), with significant month x age ($P = 0.001$) and location x age ($P = 0.005$) interactions. The age x month interaction was caused by low burdens on newborn lambs relative to yearlings and adults in December, and higher burdens on yearlings in April, June and October. The location x age interaction resulted from high burdens on yearlings at Skukuza compared to those on yearlings in the Biyamiti region, and on lambs and adults at Skukuza. The intensity of infestation on lambs and adults did not differ between Skukuza and the Biyamiti region, and there was no difference between the age classes in the latter region. The total tick burdens of the adult male and female impalas did not differ significantly ($P = 0.38$).

Amblyomma hebraeum

Adult *A. hebraeum* prefer large herbivores as hosts, whereas the immature stages feed on these animals and on a variety of smaller herbivores, leporids and ground-nesting birds (Theiler 1962; Norval 1983; Horak, MacIvor, Petney & De Vos 1987). Impalas, which we consider to be medium-sized herbivores, are excellent hosts of the immature stages and harbour virtually identical burdens to those of greater kudus in the KNP (Horak *et al.* 1992; Horak 1998).

All the impalas were infested with *A. hebraeum* larvae and nymphs in 1980/81. The intensity of infestation of both stages was higher at Skukuza and Crocodile Bridge than in the Biyamiti region ($P \leq 0.001$), but the intensity of infestation did not differ significantly among Skukuza, Biyamiti and Pafuri in July 1980 ($P = 0.14$). All the yearling males were infested with nymphs and 96 % were infested with larvae at Skukuza in 1992/93, but the intensities of infestations of both stages were significantly lower ($P < 0.001$) than in 1980/81, reflecting the low number of questing larvae in 1992/93 (Horak *et al.* 1995b). Only 67 % of the yearling males collected at Pafuri during 1992/93 were infested with larvae, and the same percentage with nymphs. The prevalence and intensities of infestation of both stages were lower at Pafuri than at Skukuza ($P \leq 0.006$). This corresponds with observations on scrub hares, *Lepus saxatilis* (Horak, Spickett, Braack & Penzhorn 1993), that the intensity of infestation of *A. hebraeum* was lower in the north of the KNP.

While impalas appear to be good hosts for the immature stages, they are poor hosts for adult *A. hebraeum*. The prevalence of adults was 31.7 % in 1980/81, and did not differ among locations ($P \geq 0.19$). The largest infestation was seven ticks, with 33 of the 44 infested impalas only harbouring one or two ticks. At Skukuza the prevalence of *A. hebraeum* adults was significantly higher ($P < 0.001$) in 1980/81 (46 %) than in 1992/93 (9 %), but the prevalence of adults did not differ between Skukuza and Pafuri in 1992/93. The maximum infestation in 1992/93 was two ticks, and no females were collected.

The intensity of infestation of *A. hebraeum* larvae varied significantly by month ($P < 0.001$) at Skukuza and in the Biyamiti region in 1980/81. There appeared to be two peaks of infestation, one from April to June, and the other during November and December (Fig. 3). The intensity of infestation was significantly higher at Skukuza than in the Biyamiti region from June to August ($P < 0.05$). The seasonal patterns of *A. hebraeum* larvae did not differ significantly ($P > 0.18$) between Skukuza and Crocodile Bridge, or between 1980/81 and 1992/93 at Skukuza. The seasonal pattern was similar at Skukuza and Pafuri from March to August 1992, but the intensity of infestation increased at Skukuza in October 1992 and declined at Pafuri. The intensity of infestation remained lower at Pafuri through April 1993. The intensity of infestation of *A. hebraeum* nymphs was significantly higher ($P < 0.001$) in late winter than in the summer. The seasonal patterns of occurrence of nymphs were similar at Skukuza in 1980/81 and 1992/93, and at Skukuza and Pafuri in 1992/93. The prevalence of adults did not differ seasonally in any of the collections ($P > 0.2$).

In earlier surveys in the KNP there was no clear pattern of seasonal abundance of the immature stages of *A. hebraeum* on greater kudus, scrub hares and helmeted guineafowls, *Numida meleagris* (Horak, Spickett, Braack & Williams 1991; Horak

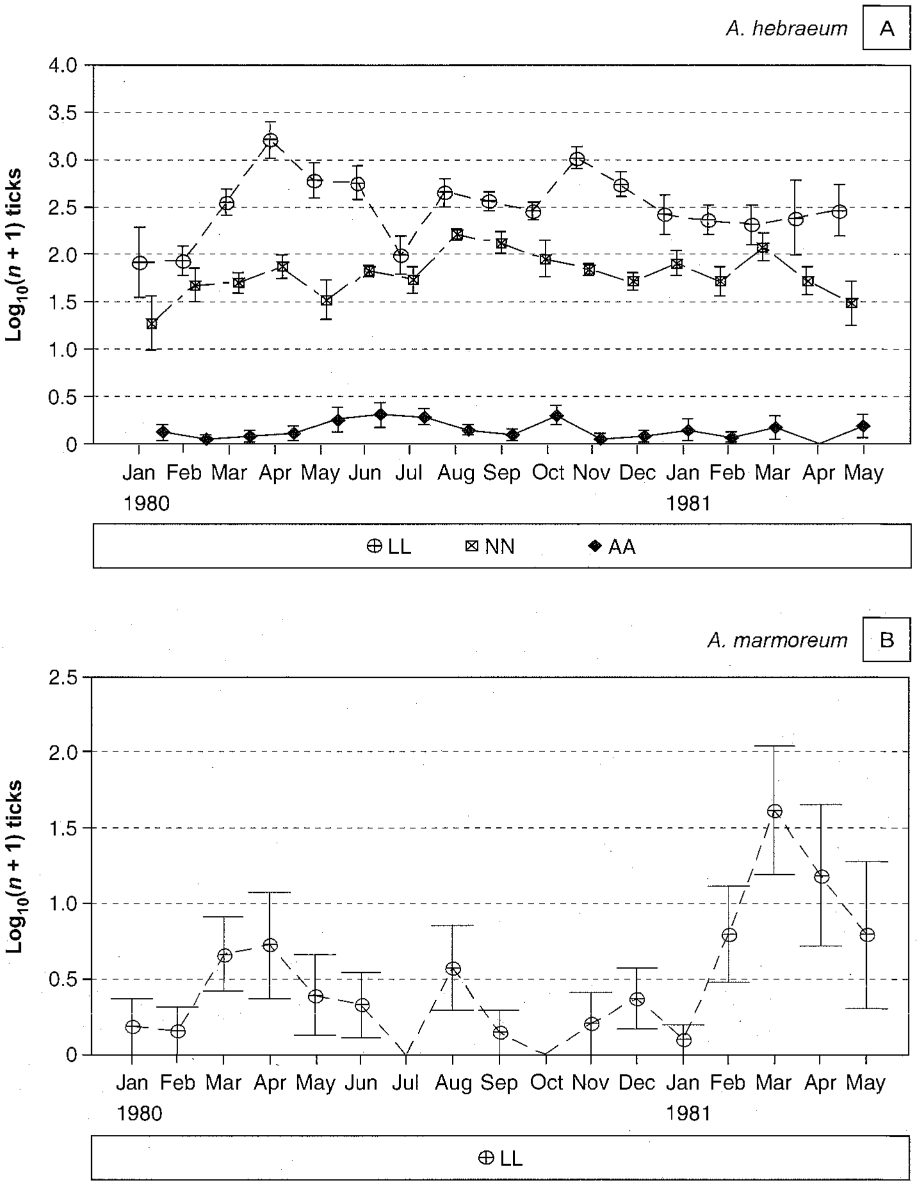

FIG. 3 Seasonal pattern of the intensity of infestation of [A] all life stages of *Amblyomma hebraeum* (x ± 1SE), and [B] larvae of *Amblyomma marmoreum* (x ± 1SE) on impalas at Skukuza and in the Biyamiti region during 1980/81. No lambs were collected after January 1981 and no yearlings after February 1981. The monthly sample at each locality ranged from two to six or seven impalas

et al. 1992; 1993). There were apparent peaks on warthogs, *Phacochoerus africanus* (Horak, Boomker, De Vos & Potgieter 1988b), and Burchell's zebras, *Equus burchellii* (Horak, De Vos & De Klerk 1984), but these seasonal patterns differ from those observed on impalas. The apparent seasonal patterns on some host species may be a function of the animals selected in the survey rather than the number of questing ticks as there does not appear to be a seasonal pattern in the number of questing *A. hebraeum* larvae (Spickett, Horak, Van Niekerk & Braack 1992).

The intensity of infestation of *A. hebraeum* larvae did not differ significantly among age classes (P = 0.20), but the intensity of infestation of nymphs was significantly higher on yearlings and adult impalas than on lambs ($P < 0.001$). The prevalence of adults was also significantly higher (P = 0.017) on yearlings (40 %) and adults (43 %) than on lambs (11.5 %). The intensities of infestations of larvae and nymphs did not differ significantly between the sexes in the adult animals ($P \geq 0.88$), but the prevalence of *A. hebraeum* adults was significantly higher ($P = 0.02$) on adult males (54 %) than on adult females (26 %). The higher prevalence and intensity of infestation of *A. hebraeum* adults on adult animals, and on adult males in particular, are consistent with the patterns reported for impalas in Swaziland (Gallivan *et al.* 1995) and kudus in the KNP (Horak *et al.* 1992).

The intensities of infestations of *A. hebraeum* larvae and nymphs did not differ significantly among the impalas examined at Skukuza in 1980 and those examined at the same locality during the 1982 drought. However, both the prevalence (100 %) and intensity of infestation of adults were significantly higher ($P < 0.002$) on the "terminal" impalas in 1982 than on the apparently healthy animals and on the impalas examined in 1980. In Swaziland, impalas infested with *A. hebraeum* adults were in poorer condition than uninfested animals, and the highest intensities of infestation with adult ticks were on adult males at the end of the dry season and after mating, periods in which these animals were already in poor condition (Gallivan *et al.* 1995). This suggests that the infestation may be secondary to the loss of resistance in stressed animals rather than a primary effect.

Amblyomma marmoreum

Amblyomma marmoreum prefers tortoises as hosts in all its stages of development (Norval 1975; Dower, Petney & Horak 1988), but the immature stages will feed on other reptiles and the larvae will also feed on carnivores, herbivores, leporids and ground-nesting birds (Norval 1975; Horak *et al.* 1987). In 1980/81, 37.6 % of the impalas were infested with *A. marmoreum* larvae. The prevalence was lower than that on helmeted guineafowls and scrub hares, but higher than on kudus examined in the KNP (Horak *et al.* 1991; 1992; 1993).

The intensity of infestation of *A. marmoreum* larvae on impalas ranged from 4–235, but 71 % of the infested animals harboured fewer than 50 larvae. The prevalence was significantly higher ($P = 0.001$) at Skukuza (34.6 %) than in the Biyamiti region (8.0 %). However, it did not differ among adult males at Skukuza, Crocodile Bridge and the Biyamiti region. This apparent contradiction occurred because the prevalences of *A. marmoreum* larvae on lambs and yearlings were much higher at Skukuza (50 %) than in the Biyamiti region (8 %) while the prevalence on adult impalas did not differ significantly between the two areas ($P = 0.24$). The prevalence at Skukuza did not differ significantly between 1980/81 and 1992/93, but the intensity of infestation was marginally higher in 1980/81 than in 1992/93 ($P = 0.07$). Prevalence at Skukuza in 1992/93 (48 %) was significantly higher ($P = 0.004$) than at Pafuri (9.5 %). This is similar to the differences recorded on scrub hares at Skukuza and in the north of the KNP (Horak *et al.* 1993). Only two impalas, both at Skukuza in 1981, were infested with *A. marmoreum* nymphs.

The prevalence and intensity of infestation of *A. marmoreum* larvae did not differ significantly ($P \geq 0.25$) on impalas at Skukuza and in the Biyamiti region from January 1980 to January 1981. However, the intensity of infestation was higher from February to May 1981 (Fig. 3). The pattern was similar in the 1992/93 ($P = 0.51$) samples where the intensity of infestation was higher in March and April in 1993 than in 1992. The higher larval burdens from March to May reflect the seasonal pattern of questing larvae on the vegetation in the park during these months (Spickett *et al.* 1992), and are similar to the patterns recorded on helmeted guineafowls, greater kudus and scrub hares in the KNP (Horak *et al.* 1991; 1992; 1993).

The prevalence and intensity of infestation of *A. marmoreum* larvae did not differ significantly among age classes ($P \geq 0.10$), or between sexes in the adult impalas ($P = 0.97$). The intensity of infestation of *A. marmoreum* larvae was higher on the "terminal" impalas in the 1982 drought at Skukuza than on the apparently healthy animals ($P = 0.05$). It was also marginally higher ($P = 0.08$) on the impalas examined in 1980 than on the apparently healthy animals in 1982.

Amblyomma tholloni

African elephants, *Loxodonta africana*, are the preferred hosts of all stages of *A. tholloni*, but the immature stages will also infest birds, reptiles, other wild mammals, and domestic cattle, sheep and goats (Theiler 1962; Norval 1983; Walker 1991). The recovery of nymphs from two impalas at Pafuri must be viewed as accidental infestations in a habitat in which there are many elephants.

Boophilus decoloratus

All the impalas were infested with *B. decoloratus*. Considering their relatively small size, impalas are remarkably good hosts of this tick as the burdens in the Biyamiti region were similar to those on greater kudus in the same region (Horak *et al.* 1992; Horak 1998). *Boophilus decoloratus* accounted for 5.6–98.6 % (mean = 57.8 %) of the total tick burden on individual impalas, and also accounted for most of the tick burden on blue wildebeest, *Connochaetes taurinus*, Burchell's zebras and greater kudus in the KNP (Horak *et al.* 1983b; 1984; 1992). However, questing larvae of *B. decoloratus* are not the most abundant species on the vegetation in the Crocodile Bridge region or at Skukuza (Spickett *et al.* 1992; Horak *et al.* 1995b; Spickett, Horak, Heyne & Braack 1995; Horak 1998), even though it was the most common tick on impalas at both localities (Table 2). Its predominance on host animals is probably because it is present throughout the year in the KNP, infests a wide range of medium to large-size ungulates, and, because it is a one-host tick, survival from one developmental stage to the next is high (Baker & Ducasse 1967; Mason & Norval 1980; Horak *et al.* 1983a; 1984; 1992).

The one-host life cycle strategy of *B. decoloratus* reduces the losses between developmental stages that occur in the multi-host ticks during their moults off the host. The mean ratio of *B. decoloratus* larvae to nymphs to adults on all the impalas examined in the KNP was 3.49:1.69:0.00, and the ratio of males to females 1.97:1.00. These ratios imply a very satisfactory transition from one developmental stage to the next on impalas. Colborne (1989) recorded a ratio of 2.31:1.31:1.00 for larvae to nymphs to adults and a ratio of males to females of 1.89:1.00 on impalas in the south-eastern lowveld of Zimbabwe. The ratio of larvae to nymphs to adults on impalas is also within the range recorded on Burchell's zebras, bushbuck, *Tragelaphus scriptus* and greater kudus in the KNP (Horak *et al.* 1983a; 1984; 1992).

In 1980/81 the intensity of infestation was higher and *B. decoloratus* accounted for a greater proportion of the tick burden in the Biyamiti region than at Skukuza ($P \leq 0.001$). At Skukuza the intensity of infestation was lower in 1992/93 than in 1980/81, and *B. decoloratus* accounted for a lower proportion of the total tick burden ($P < 0.001$). The intensity of infestation did not differ significantly between Skukuza and Pafuri in 1992/93, but *B. decoloratus* accounted for a higher proportion of the total tick burden at Pafuri ($P = 0.001$). (The latter observation appears to contradict the data in the tables. However, the tabulated data summarize all of the ticks collected, whereas this compares the percentages on individual animals). The intensity of infestation was higher on adult males in the Biyamiti region than at Crocodile Bridge, and on impalas in the Biyamiti region than at Pafuri in July 1980, but the differences were not statistically significant ($P > 0.1$). *Boophilus decoloratus* accounted for a greater proportion of the total tick burden on adult males in the Biyamiti region than at Crocodile Bridge (69 % vs 50 %; $P = 0.003$), and in the Biyamiti region than at Pafuri in July, 1980 (55 % vs 36 %), although the latter difference was not statistically significant.

The differences in the intensity of infestation of *B. decoloratus* and its proportion of the total tick burden among regions and between years may result from a number of factors, particularly climate and host availability. There appears to be a close association between the number of questing *B. decoloratus* larvae and rainfall during the preceding year at Skukuza (Horak *et al.* 1995b), and in the present study, the intensity of infestation of *B. decoloratus* appears to be higher in regions where *R. appendiculatus* predominates over *R. zambeziensis*, a tick normally found in drier areas (Norval, Walker & Colborne 1982). In addition, the availability of hosts may play an important role as exemplified by the decrease in the number of questing *B. decoloratus* larvae at Skukuza in 1992/93 following the decline in the impala population in 1992.

The seasonal patterns in the intensity of infestation of *B. decoloratus* on impalas were similar in the three southern locations. In 1980/81 the intensity was lowest in the summer and highest in the spring at Skukuza and in the Biyamiti region ($P < 0.001$; Fig. 2). *Boophilus decoloratus* accounted for the highest proportion of the total tick burden in the spring and early summer, and the lowest proportion in the late autumn and winter ($P < 0.001$). The intensity of infestation did not differ between Skukuza and the Biyamiti region in the autumn and winter, but was significantly higher in the Biyamiti region during the winter and spring. *Boophilus decoloratus* accounted for a greater proportion of the tick burden in the Biyamiti region than at Skukuza during July and August, and November and December ($P < 0.05$). The seasonal pattern was similar at Skukuza in 1980/81 and 1992/93, but *B. decoloratus* accounted for a greater proportion of the tick burden from March to September in 1980 than in 1992. The proportion was similar from October 1980 to April 1981 and from October 1992 to April 1993. In 1992/1993, the intensity of infestation was higher at Pafuri from March to August 1992, and higher at Skukuza from October 1992 to April 1993 ($P = 0.002$). Peak intensity of infestation occurred in August at Pafuri and in October at Skukuza.

The seasonal pattern in the intensity of infestation of *B. decoloratus* on impalas is similar to that on blue wildebeest, Burchell's zebras and greater kudus in the KNP (Horak *et al.* 1983b; 1984; 1992). The pre-hatch period of *B. decoloratus* eggs is longer in the cooler winter months than in the warmer months, and eggs laid in the winter hatch synchronously with those produced at higher temperatures in the spring (Robertson 1981; Spickett & Heyne 1990). The synchronous hatch and extended period of larval survival during the winter (Spickett & Heyne 1990) result in an increase in the number of questing free-living *B. decoloratus* larvae on the vegetation in the southern KNP from August to November (Spickett *et al.* 1992; Horak, Spickett & Braack 2000a). Impalas may also have a reduced resistance to tick infestation at this time because they are on a lower plane of nutrition during the dry winter season and are in poorer condition (Gallivan *et al.* 1995), which reduces their resistance to tick infestation. The higher burdens in the autumn and winter at Pafuri, and the peak in infestation during August, may be due to the 2 °C higher average winter temperature there, resulting in earlier hatching of larvae than at Skukuza.

The intensity of infestation of *B. decoloratus* was highest on yearlings and lowest on lambs ($P < 0.001$) at Skukuza and in the Biyamiti region during 1980/81. This was caused by the low intensity of infestation on newborn lambs in December and the high intensity on yearlings in April. The intensity of infestation did not differ among the age classes in the other months. The intensities of infestations of all stages of *B. decoloratus* were significantly lower on lambs in December ($P < 0.01$) indicating that the low intensity did not occur simply because there was not sufficient time for the development of the nymph and adult stages. In the other months, the intensity of infestation of larvae was lower on adult impalas ($P = 0.004$) and the intensity of infestation of adult *B. decoloratus* was lower on lambs ($P = 0.003$) while the intensity of infestation of nymphs was highest on yearlings ($P = 0.05$). The proportion of the total tick burden did not differ among the age classes ($P = 0.20$), except in December when it was significantly lower on lambs than on yearlings and adults ($P < 0.001$). The intensity of infestation and proportion of the total tick burden on adult impalas did not differ between the sexes ($P \geq 0.27$). The age/sex pattern in the distribution of *B. decoloratus* on impalas differs from that on kudus in the KNP on which there was no difference in the intensity of infestation between age classes (Horak *et al.* 1992). However, the intensity of infestation of adult *B. decoloratus* was higher on adult male kudus than on adult females. There was no difference in the intensities of infestations of any stage of development of *B. decoloratus* between the sexes of adult impalas.

The "terminal" impalas at Skukuza in the 1982 drought were more heavily infested with *B. decoloratus* than the apparently healthy animals examined at the same time or the animals examined in 1980. *Boophilus decoloratus* also accounted for a higher percentage of the total tick burden on the impalas in 1982 than in 1980 ($P = 0.002$). Comparing only the two groups of impalas examined in 1982, the percentage was marginally higher on the "terminal" animals than on the apparently healthy animals ($P = 0.07$). The collections in the 1982 drought were made during the period of peak infestations of *B. decoloratus*, and followed 2 years of above average rainfall. A reduction in resistance in impalas on a low plane of nutrition and the potentially high number of questing *B. decoloratus* larvae probably contributed to the higher burdens in 1982, particularly on the "terminal" animals.

Haemaphysalis aciculifer

The preferred hosts of the adults of this tick are wild bovids, on which it seldom occurs in large numbers (Walker 1991; Horak, Keep, Spickett & Boomker 1989). The immature stages parasitize rodents and ground-nesting birds (Horak & Boomker 1998). Since 1977 one of us (I.G.H.) has examined more than 1 200 animals belonging to many species in the KNP and has collected a total of only two male *H. aciculifer* from an eland, *Taurotragus oryx*, and 15 adults from a honey badger, *Mellivora capensis* (Horak *et al.* 1983a; Horak, Braack, Fourie & Walker 2000b), the collection of 16 larvae from a single impala must be viewed as an accidental infestation with a tick that is apparently rare in the KNP.

Hyalomma truncatum

Adult *H. truncatum* prefer large ungulates, and frequently those with thick skins as hosts (Walker 1991). This tick is abundant in the KNP judging by the large numbers of its immature stages collected from scrub hares (Horak *et al.* 1993; Horak, Spickett, Braack, Penzhorn, Bagnall & Uys 1995a), and the presence of adults on giraffes, *Giraffa camelopardalis*, and Burchell's zebras (Horak *et al.* 1983a; 1984). No adults were collected from the impalas confirming that they are not good hosts of this stage of development. The recovery of larvae from a single impala examined at Skukuza is unusual because the preferred hosts of the immature stages at this locality, and elsewhere, are scrub hares, bushveld gerbils, *Tatera leucogaster* and other rodents (Walker 1991; Horak *et al.* 1993; Braack, Horak, Jordaan, Segerman & Louw 1996).

Rhipicephalus appendiculatus

All stages of development of *R. appendiculatus* prefer the larger bovids as hosts (Yeoman & Walker 1967; Walker 1974; Norval *et al.*1982; Walker, Keirans & Horak 2000). Large numbers of adults have also been collected from lions, *Panthera leo*, in the KNP (Horak *et al.* 2000b). The immature stages are found on medium-sized and smaller antelope species, on carnivores and on hares, as well as on the larger bovids (Norval *et al.* 1982; Walker *et al.* 2000). The intensities of infestations of *R. appendiculatus* larvae and nymphs on impalas in the Biyamiti region were similar to those on greater kudus in the same area (Horak *et al.* 1992), but the intensity of infestation of *R. appendiculatus* adults was much higher on kudus.

Rhipicephalus appendiculatus larvae were present from March to October with a peak in April to June at Skukuza and in the Biyamiti region during 1980/81. Nymphs were present from March or April to December with a June to September peak, and adults were present from October to June with a February to March peak (Fig. 4). With minor differences, the seasonal patterns were similar in all locations, and were similar to those on greater kudus in the Biyamiti region (Horak *et al.* 1992) and on impalas in the Limpopo Province (Horak 1982) and in Swaziland (Gallivan & Surgeoner 1995). The seasonal patterns of *R. appendiculatus* larvae and adults were similar to their activity periods on the vegetation near Crocodile Bridge 8 to 10 years later (Spickett *et al.* 1992), but the peak activity period of the nymphs was later (August to January) on the vegetation. Although varying in intensity, *R. appendiculatus* adults were present throughout the year on the greater kudus, while their activity period appeared to be delayed on impalas in Swaziland. However, these differences, like the minor differences between locations in the present study, may reflect differences in microclimatic conditions and the spatial distributions of the hosts, two factors which influence the activity of *R. appendiculatus* (Minshull & Norval 1982).

The intensities of infestations of *R. appendiculatus* larvae and nymphs were higher in the Biyamiti region than at Skukuza during 1980/81 ($P = 0.005$ and $P < 0.001$ respectively), but the intensity of infestation of adults was higher at Skukuza ($P = 0.039$). The intensity of infestation of *R. appendiculatus* larvae was significantly higher on adult male impalas at Crocodile Bridge than at Skukuza and in the Biyamiti region ($P < 0.001$). The intensities of infestations of nymphs were higher at Crocodile Bridge and in the Biyamiti region than at Skukuza ($P = 0.008$), but the intensity of infestation of adults did not differ among the three locations ($P = 0.91$).

At Skukuza the prevalences of *R. appendiculatus* larvae, nymphs and adults on the impalas examined during 1992/93 (6.7 %, 4.4 % and 33.3 %, respectively) were significantly lower ($P = 0.02$) than in 1980/81 (48.8 %, 31.7 % and 61 %, respectively). Only four *R. appendiculatus* larvae and two nymphs were collected from each of the infested impala in 1992/93. The mean intensity of infestation of *R. appendiculatus* adults was also lower in 1992/93 than in 1980/81 ($P < 0.001$) and no adults were collected from June 1992 to January 1993. The reduction in 1992/93 may reflect both the lack of hosts (Horak *et al.* 1995b) and the reduced survival of all life stages of *R. appendiculatus* under dry conditions and reduced cover (Short, Floyd, Norval & Sutherst 1989).

The intensities of infestations of *R. appendiculatus* larvae and nymphs were higher at Pafuri and in the Biyamiti region than at Skukuza ($P = 0.04$ and 0.001, respectively) during July 1980. The prevalence of larvae was significantly higher at Pafuri ($P = 0.002$) in 1992/93, where larvae were collected in May and August 1992 and April 1993. Nymphs were present at Pafuri from May to October 1992 and in April 1993. The prevalence and intensity of infestation were higher at Pafuri than at Skukuza ($P = 0.022$ and $P < 0.001$ respectively). The prevalence of *R. appendiculatus* adults did not differ between the two locations ($P = 0.60$). The intensity of infestation was significantly higher ($P < 0.05$) at Skukuza in March 1992, but did not differ between the two locations in the other months. No adults were collected in October and December 1992.

The intensity of infestation of *R. appendiculatus* larvae did not differ among age classes ($P = 0.66$), but the intensities of infestations of nymphs and adults were higher on yearling and adult impalas than on lambs ($P = 0.001$). The intensity of infestation of larvae was higher on adult female impalas than on adult males ($P = 0.044$), whereas the intensity of infestation of the nymphs did not differ between the sexes ($P = 0.29$). The intensity of infestation of adults was higher on adult male impalas than on adult females ($P = 0.001$), particularly from March

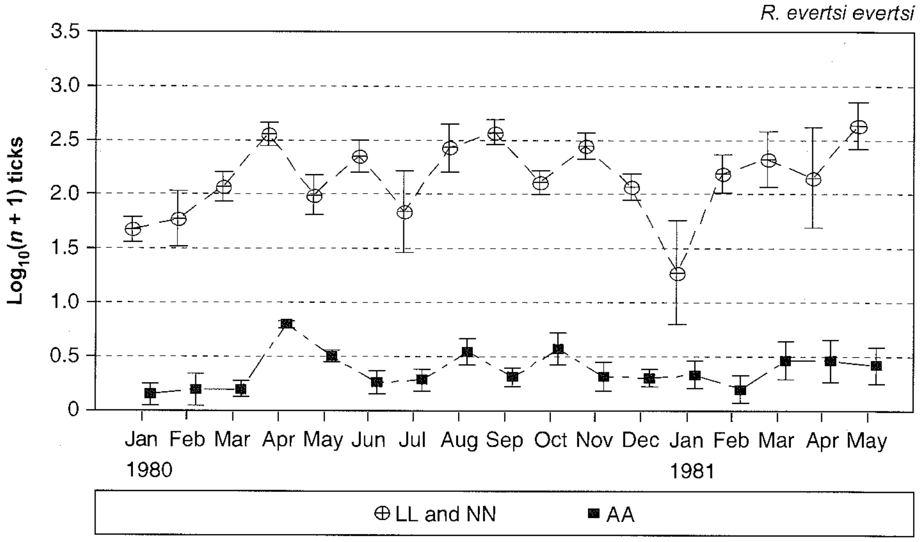

FIG. 5 Seasonal pattern of the intensity of infestation of *Rhipicephalus evertsi evertsi* (x ± 1SE) on impalas at Skukuza and in the Biyamiti region during 1980/81. No lambs were collected after January 1981 and no yearlings after February 1981. The monthly sample at each locality ranged from two to six or seven impalas

similar to the variability on impalas and kudus. The apparent peaks on impalas also differ from those on Burchell's zebras (Horak *et al.* 1984), one of the preferred hosts in the KNP. Based on the lack of a seasonal pattern and month-to-month variability in the number of questing larvae, the apparent seasonal patterns in the intensity of infestation of *R. evertsi evertsi* on impalas may simply reflect differences in the number of questing larvae and differences in the intensity of infestations among hosts.

The intensity of infestation of the immature stages of *R. evertsi evertsi* was higher in the Biyamiti region than at Skukuza in 1980/81 ($P < 0.001$), particularly during July and August, and was higher in the Biyamiti region than at Crocodile Bridge on adult male impalas ($P < 0.05$). The intensity of infestation was lowest at Pafuri in July 1980, but did not differ significantly among the three locations ($P = 0.09$). The prevalence and intensity of infestation of *R. evertsi evertsi* adults did not differ among the locations in 1980/81 ($P \leq 0.15$).

At Skukuza, the prevalences and intensities of infestations of the immature stages and adults of *R. evertsi evertsi* were significantly lower in 1992/93 than in 1980/81 ($P < 0.002$). The prevalence of the immature stages was higher ($P = 0.05$) on the yearling male impalas examined at Pafuri during 1992/93 (95.3 %) than on those at Skukuza (71 %). The intensity of infestation of the immature stages was also higher at Pafuri ($P = 0.022$), but the difference between the two locations was only significant in August 1992. The prevalence and intensity of infestation of adults did not differ significantly between the two locations 1992/93 ($P \geq 34$).

The intensity of infestation of the immature stages did not differ significantly among the age classes ($P = 0.42$), or between sexes of the adult impalas ($P = 0.72$). The prevalence of *R. evertsi evertsi* adults on adult impalas (76.5 %) was significantly higher ($P = 0.04$) than on lambs (50 %) and yearlings (56 %), and the intensity of infestation was significantly higher on adults than on lambs ($P = 0.013$). The prevalence and intensity of infestation with adult ticks did not differ between the sexes in adult animals ($P = 0.15$). These patterns are similar to those in Swaziland where the prevalence of *R. evertsi evertsi* nymphs did not differ among the age classes, the prevalence of adults was higher on adult and yearling impalas than on lambs, and the prevalence of adults did not differ between the sexes on adult impalas (Gallivan *et al.* 1995).

The intensity of infestation of the immature stages of *R. evertsi evertsi* did not differ significantly among the "terminal" impalas and the apparently healthy impalas in the 1982 drought at Skukuza and the impalas in 1980 ($P = 0.43$). The intenstity of infestation of adults was significantly higher on the "terminal" impalas than on the apparently healthy animals in 1982 ($P = 0.05$), but did not differ from the impalas examined in 1980 ($P > 0.20$).

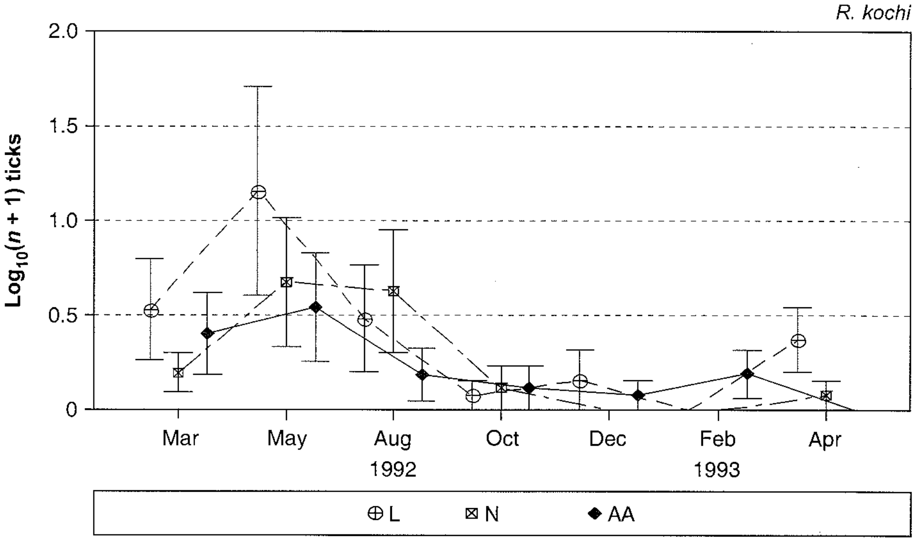

FIG. 6 Seasonal pattern of the intensity of infestation of *Rhipicephalus kochi* (x ± 1SE) on yearling male impalas at Pafuri during 1992/93. Three impalas were examined at 2–3 month intervals

Rhipicephalus kochi

Rhipicephalus kochi was only collected from impalas examined at Pafuri, and in South Africa it has been collected only in the far north-east of the Limpopo Province and of KwaZulu-Natal Province (Walker *et al.* 2000). The preferred hosts of all stages of development are medium-sized and larger antelopes and scrub hares (Walker *et al.* 2000). The prevalence and intensities of infestation of *R. kochi* larvae and nymphs were significantly higher ($P < 0.05$) from March to August 1992 than from October 1992 to February 1993 (Fig. 6). The prevalence and intensity of infestation of adults appeared to decline from March 1992 to April 1993.

Rhipicephalus pravus group

The presence on a single impala of the larvae of a *Rhipicephalus pravus*-like tick that parasitizes scrub hares in the north of the KNP (Horak *et al.* 1993) represents an accidental infestation. This tick has been described by Walker *et al.* (2000) as belonging to a *Rhipicephalus* sp. near *R. pravus*.

Rhipicephalus simus

The adults of *R. simus* prefer equids, suids, large carnivores and large ruminants as hosts, and the immature stages prefer murid rodents (Norval & Mason 1981; Braack *et al.* 1996; Walker *et al.* 2000). The collection of only one male tick each from two impalas in regions where adults are plentiful on Burchell's zebras, warthogs and large carnivores (Horak *et al.* 1984; 1988b; 2000b), supports the view that impalas are not suitable hosts. The 16 larvae collected from a single impala at Skukuza, where the majority of red veld rats, *Aethomys chrysophilus*, are infested with the immature stages of *R. simus* (Braack *et al.* 1996), also represent an accidental infestation.

Rhipicephalus zambeziensis

The preferred hosts of all stages of development of *R. zambeziensis* are domestic and wild ruminants (Norval *et al.* 1982; Walker *et al.* 2000). Numerous adults have also been collected from lions and leopards, *Panthera pardus* (Horak *et al.* 2000b). The intensities of infestations of *R. zambeziensis* larvae and nymphs on impalas in the Biyamiti region were similar to those on greater kudus (Horak *et al.* 1992), but the intensity of infestation of adults was higher on kudus, similar to the pattern for *R. appendiculatus*.

The marked seasonal changes ($P < 0.001$) in the prevalences and intensities of infestations of all stages of *R. zambeziensis* were similar to those for *R. appendiculatus*. At Skukuza and in the Biyamiti region during 1980/81, *R. zambeziensis* larvae were present from March to October with a peak from April to August, nymphs were present from May to December with a July to October peak, and adults were present in all months except July 1980, with a

February to March peak (Fig. 4). With minor differences, the seasonal patterns were similar in all locations, and were similar to those on greater kudus in the Biyamiti region (Horak *et al.* 1992)

During 1980/81, the intensities of infestations of all three stages of *R. zambeziensis* were significantly higher at Skukuza than in the Biyamiti region ($P <$ 0.007) and at Crocodile Bridge ($P < 0.05$). The intensity of infestation of larvae was also significantly higher at Skukuza and Biyamiti than at Pafuri in July 1980 ($P = 0.003$), but no nymphs or adults were collected at Pafuri at this time. The intensities of infestations of all three stages were significantly higher at Skukuza than at Pafuri in 1992/93 ($P = 0.001$), particularly during the peak periods.

In South Africa *R. zambeziensis* occurs in north-eastern Mpumalanga Province, in Limpopo Province and in the north-western regions of North West Province (Walker *et al.* 2000), and its distribution overlaps that of *R. appendiculatus* in the KNP. It is the more common species at Skukuza, whereas *R. appendiculatus* is more common at Crocodile Bridge and Pafuri. In Zimbabwe *R. zambeziensis* occurs in the lower, drier regions with mean annual rainfall of 400–700 mm, and *R. appendiculatus* is found in the higher, wetter regions with 500–2 000 mm mean annual rainfall. There is an overlap of the two species in the regions with 500–700 mm rainfall (Norval *et al.* 1982). The locations where impalas were collected in the KNP receive an average of 500–700 mm of rainfall, but the ratios of *R. zambeziensis* to *R. appendiculatus* were not consistent with the rainfall between locations. Not only was *R. appendiculatus* more common at Crocodile Bridge, which receives more rainfall than Skukuza, but also at Pafuri which receives less (Gertenbach 1980). Thus other factors such as local microclimatic conditions and habitats may influence the apparent abundance of the two species.

At Skukuza the prevalences of *R. zambeziensis* larvae and nymphs did not differ significantly between 1980/81 and 1992/93 ($P \geq 0.4$), but the intensities of infestations of both stages were significantly higher ($P \leq 0.001$) in 1980/81 than in 1992/93. There was a significant month x year interaction for both stages ($P \leq 0.035$) caused by the lower peak intensities of infestation in 1992/93. There was no difference in the prevalence or intensity of infestation of adults between years ($P \geq$ 0.54), but there was a significant month x year interaction ($P < 0.001$) as the intensity of infestation was higher from March to May 1992 than from March to May 1980, and higher from January to March 1981 than from January to March 1993. The lower intensities of infestations of *R. zambeziensis* larvae and nymphs in 1992/93 and the lower intensity of infestation of adults in 1993 probably reflect the influence of the 1992 drought on the free-living stages. However, the relative decrease was much less than the decrease in the numbers of *R. appendiculatus*, which exhibited marked decreases in the prevalences and intensities of infestation of all developmental stages. This is consistent with the greater sensitivity of *R. appendiculatus* to dry conditions.

The age/sex distribution of *R. zambeziensis* was similar to that of *R. appendiculatus*. In 1980/81 the prevalences and intensities of infestations of *R. zambeziensis* larvae and nymphs did not differ among the age classes ($P = 0.79$). The prevalence of adults did not differ among the age classes ($P =$ 0.55), but the intensities of infestations were higher on yearlings and adults than on lambs ($P < 0.001$), particularly during the peak periods. The prevalence of the three life stages of *R. zambeziensis* did not differ on adult male and female impalas ($P =$ 0.26), but the intensity of infestation of larvae was higher on adult female impalas than on adult males ($P = 0.005$), particularly during March and April 1981. The intensity of infestation of adults was higher on adult male impalas ($P = 0.029$), particularly during April and May. Combining the burdens of adult *R. zambeziensis* and *R. appendiculatus*, adult male impalas were more heavily infested than adult females ($P = 0.01$), with the largest differences from March to May. The prevalence and intensity of infestation of adult *R. zambeziensis* and *R. appendiculatus* combined was similar at Skukuza, Biyamiti and Crocodile Bridge ($P = 0.45$).

The intensities of infestations of *R. zambeziensis* larvae and adults were significantly higher ($P <$ 0.001 and $P = 0.03$ respectively) on the "terminal" impalas at Skukuza in the 1982 drought than on the apparently healthy impalas killed at the same time or on the impalas examined in 1980. The intensity of infestation of nymphs did not differ between the three groups. When the burdens of adult *R. appendiculatus* and *R. zambeziensis* were combined, the prevalence was higher ($P = 0.004$) on the impalas examined in 1980 (93 %) and on the "terminal" impalas in 1982 (90 %) than on the apparently healthy animals in 1982 (43 %). However, the intensity of infestation of the adult ticks was higher on the "terminal" impalas in 1982 than on those examined in 1980 or on the apparently healthy impalas killed in 1982 ($P = 0.01$).

LICE

Total louse burdens

The impalas were infested with five louse species, one of which, a *Linognathus* sp., has not been described. The four described species are regularly collected from impalas (Ledger 1973; 1980; Horak 1982; Horak *et al.* 1983c; Matthee *et al.* 1998). The dominant species differed among areas in the KNP, with *Damalinia elongata* the most numerous at Skukuza, *Linognathus aepycerus* the most numerous at Pafuri, *D. elongata* and *L. aepycerus* the primary species at Crocodile Bridge, and *L. aepycerus* and *Linognathus nevilli* the most common species in the Biyamiti region (Table 2).

The highest total louse burdens were recorded in the late winter/early spring (August to October) ($P =$ 0.026–0.17) and the lowest burdens in the summer (December to February) (Fig. 7). The seasonal patterns were the result of seasonal changes in the intensities of infestations of *Damalinia aepycerus* and *Linognathus aepycerus* (see below), and the decline in the summer is possibly related to the higher temperatures during this period. The seasonal pattern conforms to that observed in other studies of lice infesting impalas and other antelopes (Horak *et al.* 1983b; Horak, Sheppey, Knight & Beuthin 1986b; Matthee *et al.* 1998).

The total lice burdens were significantly higher at Skukuza than in the Biyamiti region ($P = 0.001$) in 1980/81. On adult males, the prevalence of lice at Skukuza (100 %) was significantly higher ($P = 0.031$) than in the Biyamiti region (77 %) and at Crocodile Bridge (58 %), and the total louse burden was higher at Skukuza than in the Biyamiti region and at Crocodile Bridge ($P = 0.06$). The total louse burdens were significantly higher at Skukuza during 1980/81 than during 1992/93 ($P < 0.001$) (Table 11), but did not differ significantly between Skukuza and Pafuri during the latter period ($P = 0.46$).

Lice tend to be parasites of young animals (Horak *et al.* 1983b; 1986b), and the total burdens were significantly higher on lambs and yearlings than on adult impalas ($P = 0.002$). Most louse species were present on lambs within a month of birth suggesting that they were passed from the dam. The burdens on adult impalas were higher on females than on males, but the differences were not statistically significant ($P = 0.17$).

The "terminal" impalas in 1982 had significantly higher total louse burdens than the apparently healthy impalas and those killed in 1980 ($P = 0.03$) (Table 11). The "terminal" impalas were obviously stressed and this probably lowered their resistance to lice, allowing effective and rapid translation from one developmental stage to the next. In addition, they probably lacked the energy to groom properly or conserved energy by reducing their grooming rate, thus allowing sustained levels of infestation.

Damalinia aepycerus

Damalinia aepycerus was collected at all locations in the KNP, and although it was the most numerous species on impalas in the Nylsvley Nature Reserve, Limpopo Province (Horak 1982), it was never so in the KNP. The preferred biotopes of *D. aepycerus* are the body and tail, with 60.4 % of the population present in the former and 36.0 % in the latter site (Matthee *et al.* 1998).

The intensity of infestation of *D. aepycerus* was significantly higher at Skukuza than in the Biyamiti region and at Crocodile Bridge in 1980/81 ($P < 0.03$). At Skukuza, the intensity of infestation did not differ significantly between 1980/81 and 1992/93 ($P >$ 0.17), nor did the intensity of infestation differ significantly between Skukuza and Pafuri during 1992/93 ($P = 0.34$). In 1980/81 there were two apparent peaks in the intensity of infestation (Fig. 7), one in April or March caused by high infestations on lambs and yearlings, and a more generalized peak in the late winter/spring (August to October). However, in 1992/93 the peak infestations occurred from March to May 1992 and the intensity of infestation declined through 1993. There was no clear seasonal pattern in the intensity of infestation on impalas in the Nylsvley Nature Reserve (Horak 1982), while Matthee *et al.* (1998) reported the highest intensities of infestation in February and July on impala ewes examined on Letaba Ranch, Limpopo Province during February, July and October.

The intensity of infestation of *D. aepycerus* was higher on lambs and yearlings than on adult impalas ($P = 0.065$). Infestation of lambs occurred within a month after birth. The prevalence and intensity of infestation on adult impalas did not differ significantly between sexes ($P = 0.12$). The prevalence and intensity of infestation did not differ among the three groups of impalas at Skukuza compared for the effects of the 1982 drought ($P =$ 0.18 and 0.81 respectively). The prevalence of adult lice was higher on the "terminal" and apparently healthy impalas in the 1982 drought (100 % and 90 % respectively) than on those examined in

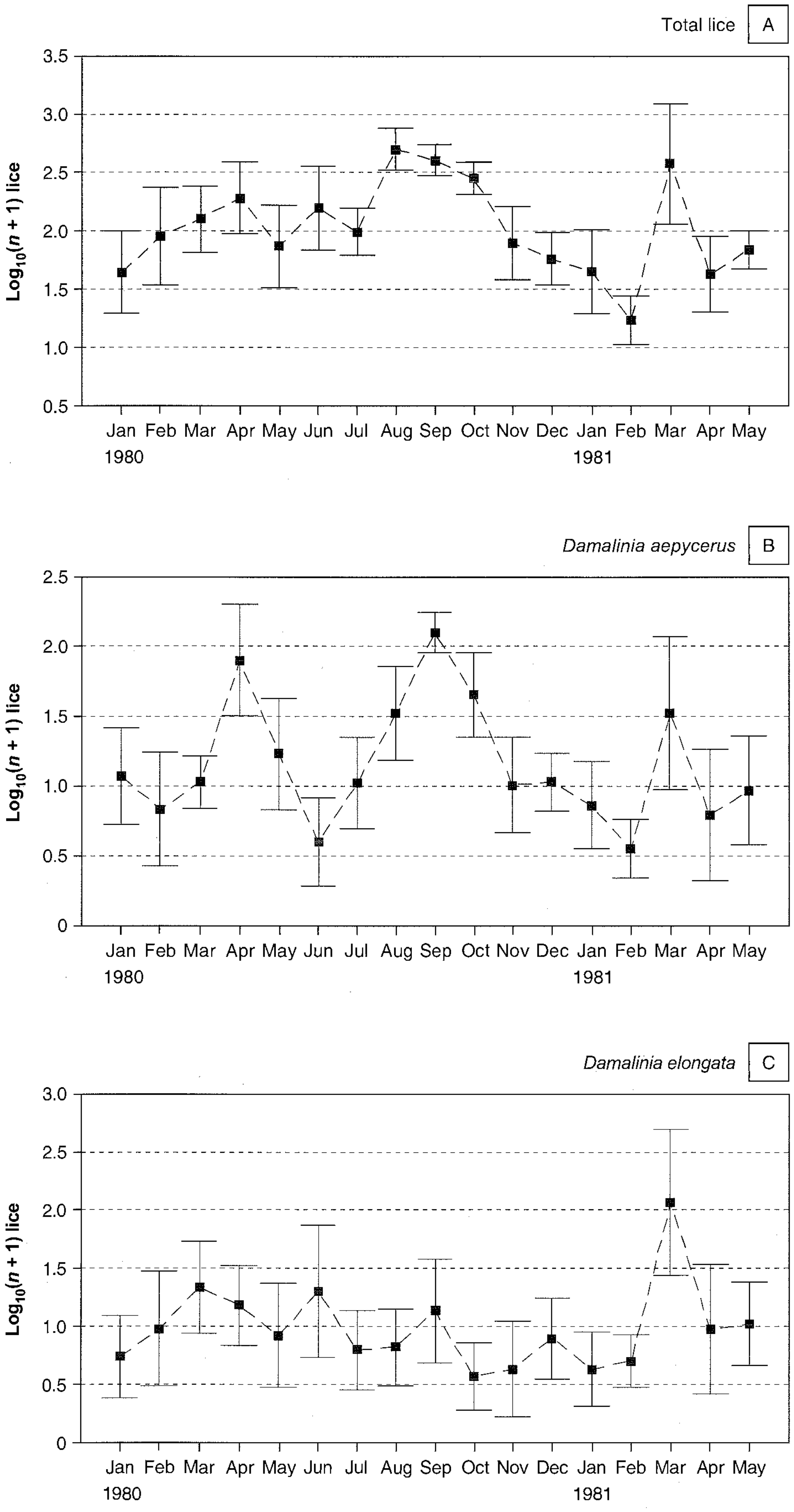

FIG. 7

Seasonal pattern of the intensity of infestation of [A] the total lice burden (x ± 1SE), [B] *Damalinia aepyceus* (x ± 1SE), and [C] *Damalinia elongata* (x ± 1SE) on impalas at Skukuza and in the Biyamiti region during 1980/81. No lambs were collected after January 1981 and no yearlings after February 1981. The monthly sample at each locality ranged from two to six or seven impalas

1980 (57 %), but the intensity of infestation did not differ among the three groups (*P* = 0.13).

Damalinia elongata

Damalinia elongata was the most numerous louse species on impalas at Skukuza in 1980/81 and 1992/93, and accounted for much of the higher louse burden at this locality in 1980/81. The prevalence and intensity of infestation were significantly higher ($P > 0.014$) at Skukuza than in the Biyamiti region in 1980/81. Although the intensity of infestation was higher on adult male impalas at Skukuza than at Crocodile Bridge, the difference was not statistically significant ($P > 0.1$). The prevalence of *D. elongata* at Skukuza did not differ significantly between 1980/81 and 1992/93 ($P > 0.25$), but the intensity of infestation was significantly higher in 1980/81 than in 1992/93 ($P = 0.004$). The intensity of infestation was similar at Skukuza and Pafuri in July 1980, but only two adult *D. elongata* were collected at Pafuri in 1992/93.

There was no seasonal pattern in the prevalence or intensity of infestation of *D. elongata* (Fig. 7). Lambs were infested by 2 months of age. The intensity of infestation was higher on yearlings than on adult impalas ($P = 0.044$), with the most pronounced differences at Skukuza. The prevalence and intensity of infestation on adult impalas did not differ significantly between sexes ($P > 0.31$). At Skukuza, the prevalence and intensity of infestation did not differ among the three groups of animals compared to assess the effect of the 1982 drought ($P = 0.46$). The intensity of infestation appears to be much higher on the "terminal" impalas, but one individual accounted for > 91 % of the total burden, and only four of ten "terminal" animals were infested.

Linognathus aepycerus

Even though the greatest numbers of *L. aepycerus* were collected from the body, this louse appears to be spread fairly evenly over the whole skin surface if the much larger surface area of the body, as opposed to those of the head, neck, legs and tail is taken into account (Matthee *et al.* 1998). It was the most common louse at Pafuri, and was also common in the Biyamiti region and at Crocodile Bridge. The prevalence of *L. aepycerus* on adult male impalas did not differ between Skukuza, the Biyamiti region and Crocodile Bridge in 1980/81 ($P > 0.3$), but the intensity of infestation was marginally higher at Skukuza than in the Biyamiti region ($P = 0.078$). At Skukuza the prevalence of *L. aepycerus* did not differ significantly between 1980/81 and 1992/93 ($P > 0.58$), but the intensity of infestation was higher in 1980/81 than in 1992/93 ($P = 0.02$). The prevalence of infestation (100 % and 87.5 % respectively) did not differ significantly ($P = 0.12$) between Pafuri and Skukuza in 1992/93, but its intensity was significantly higher at Pafuri than at Skukuza ($P < 0.02$).

There was a strong seasonal pattern in both the prevalence and intensity of infestation ($P < 0.02$) of *L. aepycerus* at Skukuza and in the Biyamiti region during 1980/81, with the highest prevalence and intensity of infestation from July to October (Fig. 8). The intensity of infestation was similar in the two areas from July to October, but tended to be higher at Skukuza in the other months. The seasonal pattern was similar at Skukuza in 1980/81 and 1992/93, but there was a significant month x location interaction between Skukuza and Pafuri in 1992/93. The intensity of infestation at Pafuri declined from March 1992 to February 1993, with only a slight increase in October 1992, whereas the pattern at Skukuza was similar to that in Fig. 11. Matthee *et al.* (1998) recorded the highest intensity of infestation with *L. aepycerus* during October on Letaba Ranch, but there was no clear seasonal pattern on impalas in the Nylsvley Nature Reserve (Horak 1982).

Lambs were infested with *L. aepycerus* within the first month after birth, and the prevalence and intensity of infestation were significantly higher on lambs than on adult impalas ($P \leq 0.004$). The prevalence and intensity of infestation on adult animals did not differ significantly between the sexes ($P > 0.16$). The prevalence and intensity of infestation of *L. aepycerus* were higher on impalas in the 1982 drought than on the animals examined in 1980 ($P \leq 0.04$), but did not differ ($P > 0.1$) between the "terminal" and the apparently healthy animals in 1982.

Linognathus nevilli

Linognathus nevilli was originally collected and described from around the feet of impalas (Ledger 1973), and is most commonly found on the feet and hind legs (Matthee *et al.* 1998). Small numbers may also be present on the head, neck and body, possibly transferred there when these regions are scratch-groomed with the hind feet, an action illustrated by Mooring (1995).

The prevalence and intensity of infestation of *L. nevilli* did not differ between Skukuza, the Biyamiti region and Crocodile Bridge in 1980/81 ($P > 0.3$). At Skukuza, the prevalence was marginally higher

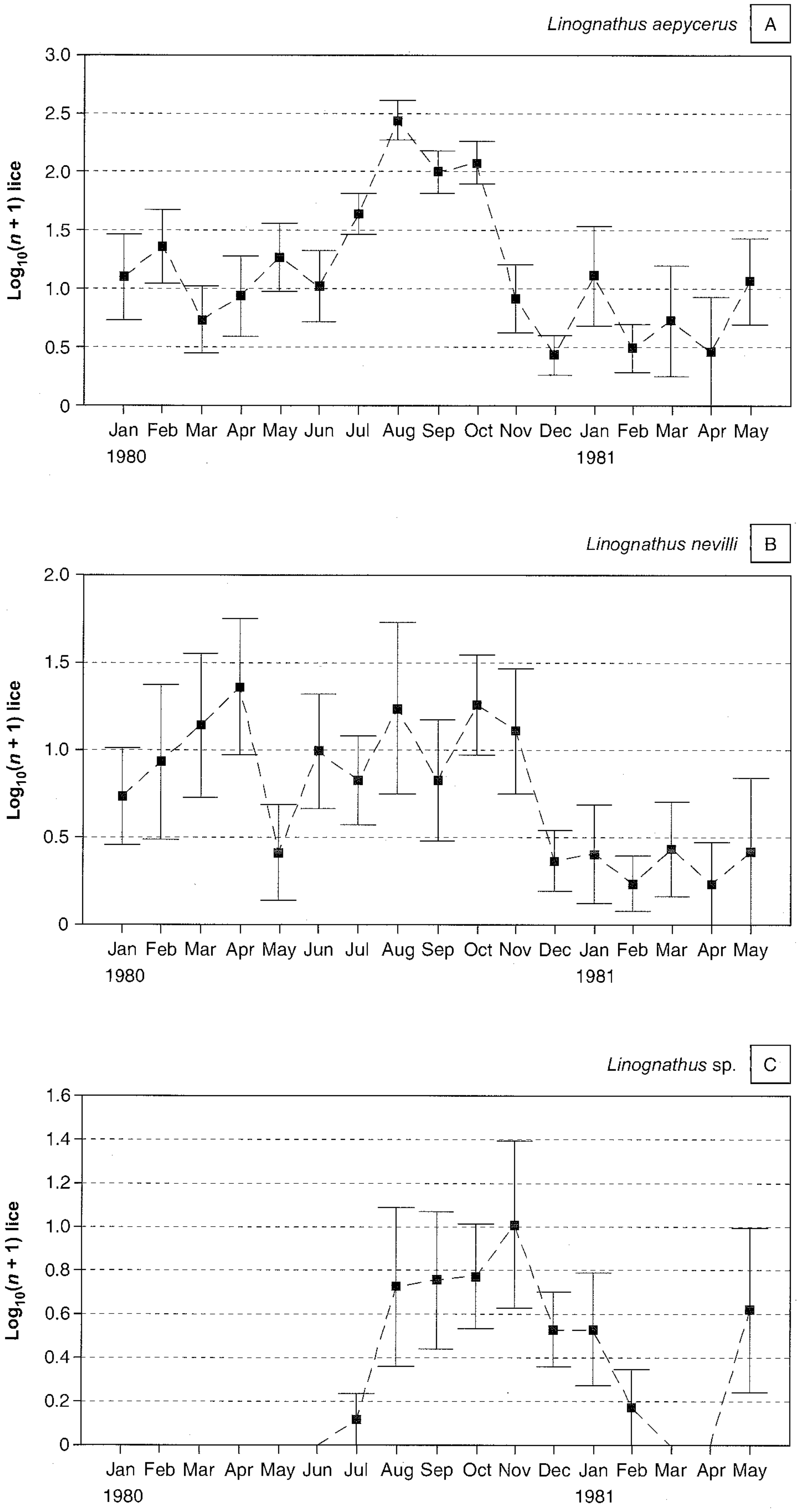

FIG. 8

Seasonal pattern of the intensity of infestation of [A] *Linognathus aepycerus* (x ± 1SE), [B] *Linognathus nevilli* (x ± 1SE), and [C] *Linognathus* sp. (x ± 1SE) on impalas at Skukuza and in the Biyamiti region during 1980/81. No lambs were collected after January 1981 and no yearlings after February 1981. The monthly sample at each locality ranged from two to six or seven impalas

($P = 0.09$) and the mean intensity of infestation was significantly higher ($P < 0.001$) in 1980/81 than in 1992/93. The prevalence did not differ significantly between Pafuri and Skukuza ($P = 0.15$), but the intensity of infestation was significantly higher at Pafuri ($P = 0.023$).

Although there were two apparent peaks, one in the late summer and early autumn, and another in the late winter and spring, there was no clear seasonal pattern in the intensity of infestation of *L. nevilli* at Skukuza and in the Biyamiti region during 1980/81 (Fig. 8). The seasonal patterns at Skukuza were statistically significant ($P = 0.008$) in the comparison of 1980/81 and 1992/93, and were more pronounced in 1980/81. No seasonal pattern was evident in the comparison of Skukuza and Pafuri in 1992/93 ($P = 0.41$). The prevalence of *L. nevilli* was significantly higher ($P < 0.001$) on lambs (81 %) and yearlings (68 %) than on adult impalas (37 %), and the intensity of infestation was significantly higher on lambs than on yearlings ($P < 0.05$), and higher on yearlings than on adult impalas ($P < 0.01$). No *L. nevilli* were collected from lambs until they were a month old. The prevalence and intensity of infestation of *L. nevilli* were significantly higher on adult female impalas than on adult males ($P \leq 0.006$).

Although the prevalence and intensity of infestation of nymphs were higher on the "terminal" impalas than on the apparently healthy animals in 1982 ($P = 0.05$ and 0.09, respectively), the prevalence and intensity of infestation of *L. nevilli* did not differ significantly between the three groups of animals ($P = 0.21$).

Linognathus sp.

Although this louse accounted for only a small percentage of the lice collected, it was common, with an overall prevalence of 27.4 %. The prevalence and intensity of infestation did not differ between Skukuza and the Biyamiti region in 1980/81, or between Skukuza and Pafuri in 1992/93 ($P = 0.35$). At Skukuza the prevalence did not differ between 1980/81 and 1992/93 ($P = 0.74$) but the intensity of infestation was higher in 1980/81 than in 1992/93 ($P = 0.01$). The prevalence was considerably lower ($P = 0.004$) on adult male impalas (9 %) than on adult females (39 %), and none were collected from the adult males at Crocodile Bridge.

The intensity of infestation of *Linognathus* sp. peaked in late winter to early summer (Fig. 8). None were collected at Skukuza or in the Biyamiti region from January to June 1980, but they were present during some of these months in 1981 and 1992/93. The1992/93 peak at Skukuza occurred in September and was of shorter duration than the peak in 1980/81. The prevalence of *Linognathus* sp. did not differ among age classes ($P = 0.44$), but the intensity of infestation was higher on lambs than on yearlings and adults ($P = 0.01$). Infestation of the lambs took place within the first month after birth. The prevalence and intensity of infestation did not differ among the "terminal" and apparently healthy impalas examined during the 1982 drought and those examined in 1980 ($P = 0.49$).

FLIES

The impalas were infested with the hippoboscid flies *Hippobosca fulva* and *Lipoptena paradoxa*.

Hippobosca fulva

According to Haeselbarth *et al.* (1966) the main hosts of *H. fulva* are probably small antelopes such as steenbok, *Raphicerus campestris*, common duikers, *Sylvicapra grimmia*, and Kirk's dik-diks, *Madoqua kirkii*, with impalas also being infested. However, we have not collected this fly from steenbok or common duikers in South Africa (I.G.H. unpublished observations 1999), and although they were collected from impalas in Swaziland, none were collected from common duikers (Gallivan & Surgeoner 1995).

The *H. fulva* collected in the current surveys do not represent the actual numbers infesting impalas in the KNP. Large numbers of these flies are visible on the white underside and perineum of impalas, where they are frequently mistaken for ticks. However, when the impalas were shot, many of them took flight and only those still present in the haircoat were collected when the carcasses were processed for tick recovery.

The prevalence and intensity of infestation of *H. fulva* were significantly higher ($P = 0.003$) on impalas in the Biyamiti region than at Skukuza during 1980/81. On adult males the prevalence was higher ($P = 0.05$) in the Biyamiti region (62 %) than at Skukuza (29 %) and Crocodile Bridge (17 %), but the intensity of infestation did not differ significantly among the three locations ($P = 0.10$). The prevalence and intensity of infestation of *H. fulva* were significantly lower (P 0.001) in spring and mid-summer than in autumn and winter (Fig. 9) on the impalas at Skukuza and in the Biyamiti region during 1980/81. The seasonal pattern in the intensity

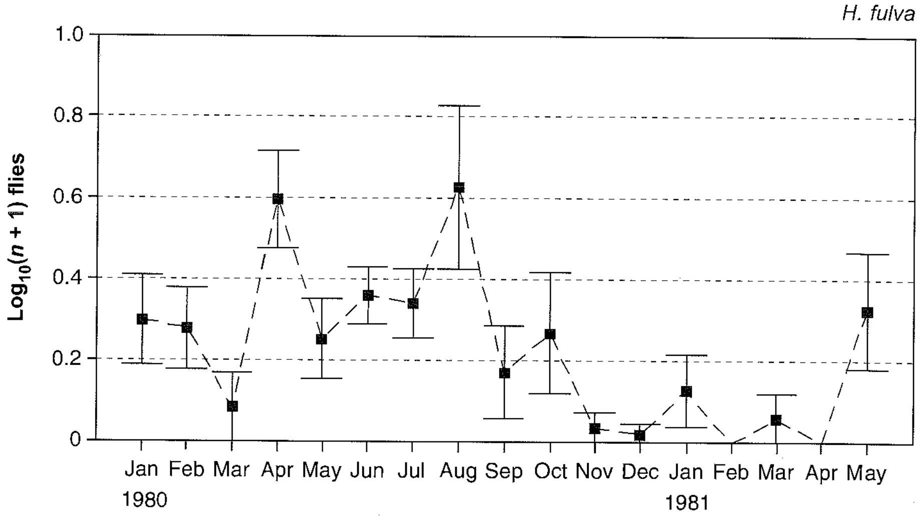

FIG. 9 Seasonal pattern of the intensity of infestation of *Hippobosca fulva* (x ± 1SE) on impalas at Skukuza and in the Biyamiti region during 1980/81. No lambs were collected after January 1981 and no yearlings after February 1981. The monthly sample at each locality ranged from two to six or seven impalas

of infestation of *H. fulva* on impalas at these localities during 1980/81 was almost the exact opposite to that noted for *L. paradoxa* on greater kudus in the Biyamiti region (Visagie, Horak & Boomker 1992). These different seasonal patterns could reflect differences in the months during which the majority of flies of the two species emerge from pupae, or differences in seasonal habitat usage by the two host species.

The prevalence and intensity of infestation of *H. fulva* did not differ among age classes ($P > 0.43$), or between the sexes of adult impalas ($P > 0.26$). Prevalence did not differ among the groups of impalas examined during the drought of 1982 and the group examined during 1980 at Skukuza ($P = 0.44$), it was, however, low during the months in which these animals were examined.

Lipoptena paradoxa

Lipoptena paradoxa is common on nyalas, bushbuck and greater kudus, and is also frequently encountered on common duikers (Visagie *et al.* 1992). All these antelopes utilize woodland habitats (Skinner & Smithers 1990). Once the fly has found a host its wings break off and it becomes a permanent parasite. Only five impalas examined during 1980/81 were infested with *L. paradoxa*, one in the Biyamiti region and four at Skukuza, and no flies were collected from adult male animals at Crocodile Bridge. Its presence on impalas must be regarded as coincidental as they frequently share woodland habitats with greater kudus.

General discussion

This paper summarises the results of several collections of arthropod parasites of impalas made over a 13-year period in the KNP. Despite differences in the age and sex composition of the animals in the surveys, we were able to examine the effects of location, season, age, sex, and two droughts. The seasonal patterns for each species of tick and louse are discussed above. The remaining factors are summarized below.

There were several differences in the ixodid tick species among locations. *Boophilus decoloratus* was most common in the Biyamiti region, while *A. hebraeum* larvae and nymphs were most common at Skukuza and Crocodile Bridge, *A. marmoreum* larvae at Skukuza, *R. evertsi evertsi* in the Biyamiti region and at Pafuri, and *R. zambeziensis* at Skukuza. *Rhipicephalus appendiculatus* larvae and nymphs were more common in the Biyamiti region and at Crocodile Bridge and Pafuri than at Skukuza, but *R. appendiculatus* adults were most common at Skukuza. [Several of the adult ticks collected from impalas at Skukuza, and identified as *R. appendiculatus*, could actually have been *R. zambeziensis* because of the difficulty of distinguishing between these species in the adult stage (Walker *et al.* 2000)]. Rainfall and temperature are important factors determining the distribution and abundance of tick species. However, the apparent abundance of tick species was not consistent with the rainfall and temperature patterns within the KNP. Part of this inconsistency may be caused by differential habitat use within heterogenous landscape types where differences in microclimates create marked differences in tick challenge (Minshull & Norval 1982). The presence of preferred or alternate hosts may also be a factor. The higher intensity of infestation of *R. appendiculatus* adults at Skukuza differs from the patterns in the intensities of infestation of the larvae and nymphs. This may, however, be due to the difficulty experienced in specifically identifying the adults as discussed above. Impalas appear to be good hosts for the immature stages of *R. appendiculatus* but poor hosts for the adults. However, in Swaziland where impalas were the most numerous ungulate species and there were few large ungulates, they were important hosts of *R. appendiculatus* adults (Gallivan & Surgeoner 1995).

The intensities of infestation of the lice *D. aepycerus* and *D. elongata* were higher at Skukuza than in the Biyamiti region and at Crocodile Bridge, while *L. aepycerus* and *L. nevilli* were more common at Pafuri. These differences in the louse populations are not easily explained, but may be due to climatic differences, or differences in the age composition of the impala populations. At Pafuri impalas tend to become older than elsewhere in the KNP because of a lower density of lions, and very old animals in this region are often unable to groom effectively because their dental grooming apparatus has become worn down (McKenzie 1990).

It is often assumed that young animals are the most prone to infestation, but the total tick burdens, and the burdens of *B. decoloratus* and *B. decoloratus* adults, *A. hebraeum* nymphs and adults, *R. appendiculatus* nymphs and adults, *R. zambeziensis* nymphs and adults, and *R. evertsi evertsi* adults were higher on yearling and adult impalas than on lambs. In contrast, with the exception of *D. elongata*, the intensity of infestation of lice was higher on lambs. The lower burdens of *B. decoloratus* on lambs were caused by a low intensity of infestation on newborn lambs in December, and the low intensity of infestation of larvae indicates that these lambs had not yet been exposed. With the exception of *B. decoloratus*, the differences among age classes were similar to those reported for tick prevalence on impalas in Swaziland (Gallivan *et al.* 1995). The lower intensities of infestations of the nymph and adult stages of ixodid ticks on impala lambs may be a function of the higher allogrooming rate of these animals (Mooring & Hart 1992). This would presumably be effective in removing the larger nymphal and adult ticks, but less so in removing the larvae. The age distribution of lice infestation conforms to observations on other species that lice tend to be parasites of young animals and that infestation occurs early in life (Horak *et al.* 1983b; 1986b; Horak, MacIvor & Greeff 2001).

The prevalence of adult *A. hebraeum* and the intensities of infestations of adult *R. appendiculatus* and *R. zambeziensis* were higher on adult male impalas than on adult females, while the intensities of infestations of *R. zambeziensis* and *R. appendiculatus* larvae were higher on adult female impalas. The higher prevalence of adult *A. hebraeum* and intensity of infestation of adult *R. appendiculatus* on adult male impalas are similar to the pattern in Swaziland (Gallivan *et al.* 1995). Gallivan *et al.* (1995) reported an increased prevalence of *B. decoloratus* adults on male impalas, and Mooring & Hart (1995) reported increased infestations of *B. decoloratus* and *R. zambeziensis* on adult male impalas during the rut in the Omay Communal lands in Zimbabwe. The differences reported for *B. decoloratus* may be caused by variations in sampling techniques among the three studies.

The contrasts in the intensities of infestations of adult *R. appendiculatus* and *R. zambeziensis* between the sexes were most pronounced during the rut. Mooring & Hart (1995) suggest that the increase in testosterone during the rut reduces immunity in the males. However, this should cause an increase in the intensity of infestation of all stages of ticks. The intensities of infestations of *R. appendiculatus* and *R. zambeziensis* larvae were actually higher on the adult female than on the adult male impalas during the rut. The higher intensities of infestations of adult *R. appendiculatus* and *R. zambeziensis* on adult male impalas during the rut are most likely caused by a reduction in grooming activity (Mooring & Hart 1995). The higher intensities of infestations of *R. appendiculatus* and *R. zambeziensis* larvae on the adult female impalas may be the consequence of increased exposure. Adult male impalas have restricted home ranges during the rut, whereas the home range of the females encompasses several male territories (Murray 1982). Because peak activity of *R. appendiculatus* and *R. zambeziensis* larvae occurs during the rut, the mobile female impalas are more likely to be exposed to them.

In contrast to the ticks, lice tended to be more common on adult female impalas than on adult males, and the differences were statistically significant for *L. nevilli* and *Linognathus* sp. Female impalas occur in larger herds, maintain shorter distances between neighbours and allogroom more frequently than males (Mooring 1995), all factors that could facilitate the transfer of lice between individuals. Both *L. nevilli* and *Linognathus* sp. have relatively low prevalences and intensities of infestation, and increased interaction among females may be essential to maintain transmission.

The collections included two droughts, in 1982 and in 1992 (Fig. 1). The 1982 collections were made in November and early December, following an extended period of low rainfall beginning in February 1982, and the 1992/93 collections began at the end of the summer after a year of low rainfall and continued through a year of normal rainfall. Consequently the collections represent different phases of the drought. The 1982 collections were also preceded by two years of above normal rainfall and impala populations, while the 1992/93 collections were preceded by two years of below average rainfall and impala populations.

In 1982 there was an increase in the total tick and louse burdens on the "terminal" impalas, primarily because of the increase in the intensities of infestations of *B. decoloratus* and *L. aepycerus*, and the burden of *D. elongata* on one individual. There was also an increase in the intensities of infestations of adult *A. hebraeum*, *R. appendiculatus*, *R. evertsi evertsi* and *R. zambeziensis*. These patterns reflect the seasonal activity of the ticks and lice, and are consistent with a reduction in resistance in animals in poor condition. There were few differences in the tick and louse burdens between the "apparently healthy" impalas in 1982 and those examined in 1980. In 1992/93 there was a reduction in the intensities of infestations of all tick and louse species relative to 1980/81. The reductions in the louse burdens and intensities of infestations of *R. zambeziensis* larvae and nymphs were proportional to the reduction in the size of the impala population, indicating that the availability of the hosts was a major factor in maintaining ectoparasite populations. The reductions in the infestations of *A. hebraeum*, *B. decoloratus*, *R. evertsi evertsi* and *R. appendiculatus* in 1992/93 relative to 1980/81 were greater than the reduction in the impala population. The drier environmental conditions probably reduced the survival of the free-living stages of these species as there was a greater reduction in the number of questing *B. decoloratus* larvae than *R. zambeziensis* larvae (Spickett *et al.* 1995), and *R. zambeziensis* tolerates drier conditions than *R. appendiculatus*. Thus, while the collections in the 1982 drought indicate that the immediate impact of a drought may be an increase in ectoparasite infestations because of the nutritional stress, the collections in the 1992 drought suggest that a reduction in impala populations as well as reduced survival of the free-living ticks may reduce the ectoparasite burdens over time.

ACKNOWLEDGEMENTS

We are greatly indebted to the South African National Parks for placing the animals as well as their staff and facilities in the Kruger National Park at our disposal. We gratefully acknowledge the assistance of Messrs C. Cheney, J. Sithole and the late B.D. de Klerk with processing the carcasses for the recovery of ectoparasites, and that of Mrs E.L. Visser, Miss M.L. Horak and Mr A.C. Uys who assisted in the recovery of the parasites from the processed material.

This research was funded by the Faculty of Veterinary Science, University of Pretoria, the South African National Parks, the Foundation for Research Development (now the National Research Foundation), and Bayer Animal Health.

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HELMINTH AND ARTHROPOD PARASITES

Koedoe 16: *77–81* (1973).

PARASITES AND DISEASES OF CAPE MOUNTAIN ZEBRA, BLACK WILDEBEEST, MOUNTAIN REEDBUCK AND BLESBOK IN THE MOUNTAIN ZEBRA NATIONAL PARK

by

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Abstract – The results of a special survey are supplemented in this report with a review of all other applicable information on the diseases and parasites of Cape mountain zebra, black wildebeest, mountain reedbuck and blesbok in the Mountain Zebra National Park. The possible significance of some of these infections is discussed and various suggestions are made which aim at the continued and successful preservation of the Cape mountain zebra and other species in this National Park.

Infectious diseases and parasites isolated from or identified in *Equus zebra zebra* (Cape mountain zebra), *Connochaetes gnou* (black wildebeest), *Redunca fulvorufula* (mountain reedbuck), *Damaliscus dorcas phillipsi* (blesbok) in the Mountain Zebra National Park (M.Z.N.P.), are summarized in tabular form.

Babesia equi was found in blood smears of three of the five Cape mountain zebra captured and sampled (Neitz, *pers. comm.*). These animals were all heavily infested with ticks but were otherwise clinically normal. Latent infections of *B. equi* are known to flare up and produce deleterious and often fatal effects in the horse when the host animal is subjected to certain stressful conditions. Similarly wild animals, pre-immune to certain protozoal infections, may fall victim to such infections under certain circumstances. The apparent high incidence of subclinical equine babesiosis in this very rare subspecies of *Equus zebra* is therefore viewed with great concern.

The interpretation of the results of serological tests for horse sickness and equine rhinopneumonitis was complicated by the anti-complementary nature of the zebra serum as well as by other technical difficulties and

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Table 1

Parasites and infectious diseases of Cape Mountain Zebra, Black Wildebeest, Mountain Reedbuck and Blesbok in the Mountain Zebra National Park

Host	Parasite/disease		Remarks
Cape mountain zebra	Endoparasites	*Gasterophilus pecorum*	"Bots" in stomach
		G. intestinalis	"Bots" in stomach
		Anoplocephala magna	Cestode in stomach and duodenum
		Trichonema (larvae)	Found in numerous cysts in the intestinal wall
	Ectoparasites	*Rhipicephalus e. evertsi*	Heavy tick infestation
		R. glabroscutatum	Heavy tick infestation
		Hyalomma rufipes	Heavy tick infestation
		Margaropus winthemi	Heavy tick infestation
	Infectious diseases	Babesiosis (*B. equi*)	Bloodsmears positive
		Horse sickness	Results indefinite (serum anti-complimentary)
		Equine rhinopneumonitis	Results indefinite (serologically suspicious)
Black wildebeest	Endoparasites	*Haemonchus* sp.	Nematode in abomasum
		Oesophagostomum sp.	Nematode in colon
		Trichinella spiralis	Microscopic examination of digested tissues negative
	Ectoparasites	*Rhipicephalus glabroscutatum*	Ticks, especially on thin-skinned parts
		Lipoptena sepiacea	Biting fly (hippoboscid)
		Gedoelstia sp.	Larvae (L II + III) in the nasal cavity
	Infectious diseases	Bluetongue	Serological tests negative
		Rift valley fever	Serological tests negative
		Wesselsbron disease	Serological tests negative
		Protozoa	Blood smears and histological preparations negative
Mountain reedbuck	Endoparasites	*Haemonchus* sp.	Nematode in abomasum
		Nematodirus spathiger	Nematode in duodenum
		Moniezia expansa	Cestode in duodenum
		Setaria boulengeri	Nematode in abdominal cavity
		Trichinella spiralis	Microscopic examination of digested tissues negative

Table 1 (cont.)

Host	Parasite/disease		Remarks
	Ectoparasites	*Rhipicephalus glabroscutatum*	Heavy tick infestation
		Linognathus reduncae	Sucking lice (Anoplura)
		Damalinia trabeculae	Biting lice (Ischnocera)
	Infectious diseases	Bluetongue	Serological tests negative
		Rift valley fever	Serological tests negative
		Wesselsbron disease	Serological tests negative
		Protozoa	Blood smears and histological preparations negative
Blesbok	Endoparasites	*Haemonchus contortus*	Nematode in abomasum
		Nematodirus spathiger	Small red nematode in duodenum
		Cysticercus tenuicollis	Cysts on mesentery
		Trichinella spiralis	Microscopic examination of digested tissues negative
	Ectoparasites	*Rhipicephalus glabroscutatum*	Ticks
		Oestrus variolosus	Larvae (L I–III) in nasal cavities and frontal sinuses
	Infectious diseases	Bluetongue	Serological tests negative
		Rift valley fever	Serological tests negative
		Wesselsbron disease	Serological tests negative
		Protozoa	Blood smears and histological preparations negative

special tests for these and other important diseases of the Equidae obviously have to be repeated and even extended.

One young zebra foal was found to be heavily infested with various internal parasites which resulted in parasitic enteritis. Nematodes (*Trichonema* sp.) could be detected macroscopically in numerous cystic lesions in the intestinal mucosa. This particular case left very little doubt that such heavy infestations may sometimes end fatally.

Since the proclamation of the M.Z.N.P. in 1937, the zebra have increased steadily in this Park from relatively few animals to their present number of about 130 individuals. Inbreeding could already have reduced the inherent resistance of these animals to diseases and parasitism by now and may even become a bigger problem in the future if the necessary provision is not made for the introduction of sufficient new genetic material. In addition trace-element deficiencies, which seem to exist in this park, may also exert some decimating effects. Domestic horses, which may harbour infectious diseases to which the Cape mountain zebra is susceptible, are furthermore kept in this park and on adjoining farms and the possibilities of introducing and establishing new infections are therefore not excluded.

Apart from the possible introduction of sufficient new genetic material from other populations of Cape mountain zebra, the continued existence of this subspecies may expectedly be further ensured by capturing a considerable number of the animals in the M.Z.N.P., by deworming these and treating and vaccinating them against all the diseases and parasites which they may harbour or contract and to subsequently use these animals to establish a further breeding nucleus of Cape mountain zebra at another suitable and safe reserve. Decentralization of this population and active attempts at prophylactic disease and parasite control seem imperative if this subspecies is to be safely protected for the future.

Considerable numbers of other animals (i.e. more than 500 springbok) exert a severe grazing pressure on this park which was primarily proclaimed for the preservation of the Cape mountain zebra. Apart from their direct effects on the grazing and therefore the possible threat which the apparent excessive numbers of these more common species may pose to the zebra, especially during very dry years, the high population densities of these other species have already resulted in heavy parasitic infestations in themselves. This seems to be particularly true in the springbok *Antidorcas marsupialis*. Post mortem examinations on a limited number of carcasses created the impression that heavy infestations of *Cooperioides antidorci* may, under certain circumstances, be responsible for mortalities in springbok. *Nematodirus spathiger* infestations were furthermore repeatedly associated with signs of enteritis and/or intestinal catarrh in heavily infested blesbok and mountain reedbuck. *Haemonchus contortus*, which is known to infest 19 antelope species (Neitz, 1965) and can be responsible for mortalities in blesbok (own observations), has been recovered from blesbok, springbok, black wildebeest and mountain reedbuck in the M.Z.N.P.

As with the zebra, the necessary precautions should also be taken to prevent the introduction of diseases and parasites to which these other species are susceptible. Furthermore, developing problems of localized overgrazing and concomitant superinfestation of certain areas with parasites may possibly be overcome by the well planned further distribution of watering points, as well as by the provision of mineral licks at strategic places in underutilized areas. Mineral licks, if adequately utilized, may also be used as a medium for the administration of anthelmintics, should parasitism become a real threat as may be foreseen under the present circumstances.

Acknowledgements

We wish to extend our thanks and appreciation to the Director of the National Parks Board for making the study material available. Special thanks are due to Mr. A. M. Brynard and Dr. G. de Graaff, Deputy

Director and Assistant Director (Other National Parks) respectively of the National Parks Board, for special arrangements. We also thank all other personnel of the National Parks Board, as well as the Onderstepoort Veterinary Research Institute, the S.A.I.M.R. (ectoparasite studies supported financially by the S.A. Medical Research Council) and Mrs. B. Young for their invaluable assistance in collecting and/or examining the sample material.

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NOTES ON THE PARASITOLOGY, PATHOLOGY AND BIO-PHYSIOLOGY OF SPRINGBOK IN THE MOUNTAIN ZEBRA NATIONAL PARK

by

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Abstract – Thirteen species of parasitic metazoa and two protozoa have been identified. Pathological effects are described where applicable. Serological tests for virus diseases were negative but biochemical analyses revealed certain mineral deficiencies. The possible decimating effects of the former are discussed and appropriate guide lines for control suggested.

During a preliminary survey in October, 1971 in the Mountain Zebra National Park (M.Z.N.P.) near Cradock, Cape Province, 10 live and eight dead springbok, *Antidorcas marsupialis*, were captured or culled. These were examined and the necessary specimens collected for subsequent analyses. The results of this preliminary survey can be very briefly summarized as follows:

Endoparasites

Haemonchus contortus was collected from the abomasum, *Cooperioides antidorci*, *Paracooperia serrata*, *Nematodirus* sp. and *Trichostrongylus faculatus* from the duodenum, *Agriostomum equidentatum* from the colon and *Cysticercus tenuicollis* from the abdominal cavity.

Cooperioides antidorci caused extensive duodenal lesions in some of the animals and it is suspected that this parasite may, under certain circumstances, be responsible for very adverse effects on super-infested springbok. The parasites (small nematodes) were found in numerous small but macroscopically visible glistening cysts. Microscopically it could be seen that many of the duodenal crypts, containing the parasites, had become occluded and cystic. The cystic lesions were present in the mucosa as well as in the submucosa, and in the latter the parasites were in some cases

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surrounded by considerable granulomatous reaction and fibrosis. In cross section, the helminths have 10 to 14 longitudinal ridges with cross striations.

The aetiology of the abomasal erosions and ulcerations has not yet been established without doubt but it is suspected that these lesions, as well as the mixed cell abomasitis, seen in some animals, might have been due secondarily to haemonchosis.

It is also suspected that endoparasites, such as *C. tenuicollis* and *A. equidentatum* and possibly others whose migratory patterns are still unknown, while migrating through the liver at some stage of their life cycle, could have been responsible for the lesions frequently seen in this organ. These lesions included localized patches of necrosis and subacute to chronic hepatitis, as well as proliferative and granulomatous reactions and fibrosis in some portal areas. Localized segmental eosinophilic endophlebitis of the portal veins was also observed which strengthens the suspicion of migrating parasites being involved.

Ectoparasites

The ticks, *Hyalomma rufipes*, *Rhipicephalus glabroscutatum* and *R. e. evertsi* and the lice, *Linognathus euchore*, *L. armatus* and *L. bedfordi* parasitised the sampled springbok.

H. rufipes caused extensive dermal necrosis and localized, superficial mastitis in one animal. The other external parasites were not associated with any lesions.

Sarcoptes scabiei, associated with severe mange, has recently been isolated from springbok in the Kalahari Gemsbok National Park (Young and Zumpt, ms.). Springbok in the M.Z.N.P., however, seem to be free of this potentially fatal infestation.

Protozoal, viral and bacterial diseases

Examination of blood smears revealed a *Cytauxzoon* sp. (Neitz, *pers. comm.*) while mild sarcosporidiosis was diagnosed by microscopic examination of the cardiac musculature of one animal.

Serological tests on serum samples failed to show antibodies against blue tongue, Rift valley fever or Wesselsbron disease.

No specific bacterial diseases were diagnosed although one very sick and debilitated animal suffered from severe, purulent pneumonia and another from otitis externa, both conditions apparently having been due to bacterial infection.

Nutrition, biochemistry and general bio-physiology

Liver-samples were collected from five adult springbok and analysed for trace-elements according to the techniques used by Boyazoglu, Barrett, Young and Ebedes (1972). The average figures (p.p.m. on wet basis) were: Mn (4,8), Cu (11,8), Co (13,4), Zn (126), Fe (183) and Mg (118).

These results were compared with those obtained from the analyses of liver-samples of three adult springbok from the Kalahari Gemsbok National Park. From these comparisons it appears that relative deficiencies of manganese, cobalt, magnesium and especially of copper may occur in the M.Z.N.P. Values for zinc and especially for iron were, on the contrary, higher for the latter park. When compared with average results obtained from analyses of samples from 250 wild mammals of 16 different species from the Kruger and Etosha National Parks (Boyazoglu, Barrett, Young and Ebedes, 1972), deficiencies of manganese, cobalt, magnesium and especially copper again seem to occur in the M.Z.N.P.

It is suspected that deficiencies of some of these trace elements, notably of copper and cobalt, as well as a possible phosphate deficiency, severe parasitism and inbreeding may be responsible for the apparent smaller size of these springbok, compared to springbok from some places elsewhere in the Republic of South Africa or South West Africa. The macro-element survey has not yet been completed but dental and other skeletal abnormalities observed point towards a possible deficiency of phosphorus. Excessive mineral deposits in the urine of slaughtered animals (in some individuals associated with mucosal haemorrhages of the urinary bladder) suggest the possible excessive intake of dietary calcium which may result in, or aggravate phosphorus deficiency. This supposition, however, still has to be evaluated by further research.

Electrophoretic and other analyses of serum and haemoglobin samples have also not yet been completed but the considerable increase of this population from about 20 individuals (1943) to more than 1 200 animals leaves no doubt as to the possibility that a remarkable degree of inbreeding must already be present in these springbok. Pathognomic clinical signs of inbreeding which have during the past few years repeatedly been encountered in an inbred population of springbok in the Warmbaths district of the Transvaal have, however, not yet been observed in springbok of the M.Z.N.P.

General remarks

Despite the prolific and very successful numerical increase of this population over the past few years, the continued and unrestricted increase of springbok in this relatively small National Park does not seem feasible and may eventually prove disastrous*. Optimal population density has apparently been exceeded and intra and interspecific competition has already become a reality. Excessive concentrations of animals weakened by nutritional deficiencies, parasitism and inbreeding are usually extremely liable to the development of catastrophes and special attention must preferably be paid in the case of this population to the advisability and possibilities of reduction campaigns, the introduction of new genetic material, mineral supplementation and possibly also to periodic and controlled low level anthelmintic treatment via mineral licks.

Acknowledgements

We wish to extend our thanks and appreciation to the Director of the National Parks Board for making the study material available. Special thanks are due to Mr. A. M. Brynard and Dr. G. de Graaff, Deputy Director and Assistant Director (Other National Parks) respectively of the National Parks Board, for special arrangements. We also thank all other personnel of the National Parks Board, the Onderstepoort Veterinary Research Institute, the S.A.I.M.R. (ectoparasite research supported financially by the S.A. Medical Research Council) and Mrs. B. Young for their invaluable assistance in collecting and/or examining the sample material.

**Towards the end of* 1972, *the numbers of springbok were reduced by* 700 *individuals – Eds.*

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HELMINTH AND ARTHROPOD PARASITES OF BLESBOK, *DAMALISCUS DORCAS PHILLIPSI,* AND OF BONTEBOK, *DAMALISCUS DORCAS DORCAS*

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ABSTRACT

HORAK, I. G., BROWN, MOIRA R., BOOMKER, J., DE VOS, V. & VAN ZYL, ELSA A., 1982. Helminth and arthropod parasites of blesbok, *Damaliscus dorcas phillipsi*, and of bontebok, *Damaliscus dorcas dorcas*. *Onderstepoort Journal of Veterinary Research*, 49, 139–146 (1982).

The helminth burdens of 8 blesbok shot in the north-eastern Orange Free State, 8 from the eastern Cape Province, 28 from the eastern Transvaal and 3 from the central Transvaal were determined. In addition, the arthropod burdens of 11 of these animals were ascertained. Twenty-one nematode species, 2 cestode species, 6 ixodid ticks, 2 lice and the larvae of 5 oestrid flies were recovered. Three of the nematode species, 2 of the oestrid flies and 4 of the tick species had apparently not previously been recovered from blesbok.

Thirty-one bontebok culled in the south-western Cape Province were examined for endoparasites and 8 of these animals were also examined for ectoparasites. They harboured 12 nematode species, 3 ixodid ticks, a louse and the larvae of an oestrid fly. In common with some of the blesbok they were parasitized by *Dictyocaulus magnus, Longistrongylus curvispiculum, Trichostrongylus axei, Nematodirus spathiger* and the larvae of a large *Gedoelstia* sp. Five of the nematode species, the larvae of the oestrid fly species and the 3 ixodid tick species had not previously been recorded from bontebok.

INTRODUCTION

Blesbok, *Damaliscus dorcas phillipsi,* are distributed in the Cradock and Cathcart districts in the eastern Cape Province, north and north-east through the north-eastern Cape Province and the Orange Free State to the southern Transvaal. Bontebok, *Damaliscus dorcas dorcas,* formerly distributed in the south-western Cape Province in the coastal area between Caledon and Mossel Bay, now survive only in a semi-captive state on enclosed land mainly around Bredasdorp and in the Bontebok National Park (Ansell, 1971). Round (1968) has listed the helminth parasites, Zumpt (1965) the oestrid larvae and Ledger (1980) the lice recovered from these animals. Horak (1980 a) has tabulated the helminth and arthropod parasites he has recovered from blesbok, while Verster, Imes & Smit (1975) have listed the helminths they have recovered from bontebok with those recorded by Ortlepp (1961, 1962).

The seasonal prevalence of the larvae of oestrid flies and of helminths in blesbok was determined in the northern Transvaal (Horak & Butt, 1977; Horak, 1978 a), a region considered to lie outside the original habitat of these animals (Ansell, 1971). Those blesbok were grazing Sour Bushveld (Acocks, 1975) at a low stocking density with tsessebe and roan antelope and were not examined for the presence of other ectoparasites. The numbers of parasites harboured by 2 bontebok, which died a few days after translocation from the Bontebok National Park to the National Zoological Gardens, Pretoria, were determined by Verster *et al*. (1975).

The present paper reports the worm burdens and some ectoparasite burdens of blesbok in 4 small nature reserves located in the north-eastern Orange Free State, the eastern Cape Province and the eastern and central Transvaal, and of bontebok in a small park in the south-western Cape Province.

MATERIALS AND METHODS

A total of 8 blesbok were shot at various times in the Golden Gate Highlands Park (28°31′S; 28°37′E; Alt. 1 798–2 731 m) near Clarens in the north-eastern Orange Free State, a park 4 792 ha in extent and situated in a region classified as Highland Sourveld (Acocks, 1975). It contains blesbok, black wildebeest, eland, oribi, red hartebeest, springbok and Burchell's zebra. A similar number of blesbok were shot in the Mountain Zebra National Park (32°15′S; 25°41′E; Alt. 1 200–1 957 m) near Cradock in the eastern Cape Province. This park, 6 536 ha in extent and situated in Karroid *Merxmuellera* Mountain Veld replaced by Karoo (Acocks, 1975), contains blesbok, black wildebeest, eland, gemsbok, mountain reedbuck, red hartebeest, vaal ribbok, steenbok, klipspringer, springbok and Cape mountain zebra.

Twenty-eight blesbok were shot in the Rob Ferreira Nature Reserve at Badplaas (25°57′S; 30°34′E; Alt. ± 1 067 m) in the eastern Transvaal. This reserve is situated in a region classified as Piet Retief Sourveld (Acocks, 1975) and is approximately 400 ha in extent and, in addition to blesbok, contains black wildebeest, eland, impala, oribi, springbok, tsessebe and Burchell's zebra, a total of approximately 450 animals. Two animals were shot during May 1978, 11 during June and 15 during July of the same year.

Three blesbok were shot during June 1981 in the Rietvlei Nature Reserve (25°53′S; 28°17′E; Alt. ± 1 500 m) to the south-east of Pretoria in the central Transvaal. This reserve, which is approximately 3 000 ha in extent, lies within a region classified as Bankenveld (Acocks, 1975) and, in addition to blesbok, contains black wildebeest, red hartebeest, eland, springbok, duiker, steenbok, oribi and Burchell's zebra.

Eight bontebok were shot during June 1975, 9 during September 1975, 6 during March 1976 and 8 during December 1979 in the Bontebok National Park (34°02′S; 20°25′E; Alt. 90–200 m) near Swellendam in the south-western Cape Province. The park is situated in Coastal Renosterbosveld (Acocks, 1975) and has an area of 2 786 ha. In addition to bontebok, it also contains vaal ribbok, springbok, Cape grysbok, steenbok, bushbuck and grey duiker.

The lungs and some of the livers of the blesbok and some of the lungs and livers of the bontebok were processed for worm recovery as described by Horak (1978 b), while the contents of their abomasa and small intestines were sieved separately over sieves with 38 μm apertures and that of their large intestines over sieves with 150 μm apertures. The contents of the sieves were formalinized and retained for future examination. The mucosae of the abomasa and intestinal tracts of all the blesbok at Badplaas and from near Pretoria and only those of the blesbok and the bontebok shot during December 1979 near Clarens, Cradock and Swellendam were digested with pepsin and HCl.

The nasal passages and paranasal sinuses of 2 blesbok from near Clarens, 2 from Cradock, 4 from Badplaas and 3 from near Pretoria and 8 bontebok from Swellendam

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Received 7 April 1982—Editor

were examined for oestrid larvae as described by Horak (1977) and their hearts washed for the recovery of these larvae, as described by Horak & Butt (1977). The cranial cavities and brain surfaces of the same 2 blesbok from Clarens and 2 from Cradock and 3 from near Pretoria and 8 bontebok from Swellendam were also examined for oestrid larvae.

The skins of the heads and of the bodies of 4 animals at Badplaas and the 3 from near Pretoria, plus all 4 legs of each animal from below the knee and hock joints with their skin intact were immersed in a tick detaching agent*. The skin of 1 side of the head and 1 side of the body, as well as 1 front leg and 1 back leg with their skin intact, of 2 blesbok at Clarens, 2 at Cradock and 8 bontebok at Swellendam were similarly processed. Thereafter the skins and legs were stored overnight in tightly closed plastic bags. The following morning they were scrubbed with brushes with 20 mm long steel bristles and thoroughly washed. The washings were sieved through sieves with 150 μm apertures and the contents of the sieves collected and preserved with formalin for future examination.

RESULTS

The mean helminth burdens of the blesbok from the Golden Gate and Mountain Zebra Parks are summarized in Table 1.

Ten nematode species were recovered from these animals. Eight of these were present in both parks, while *Nematodirus helvetianus* was present only in the Golden Gate reserve and *Nematodirus spathiger* only in the Mountain Zebra reserve. In general, the animals in the former reserve harboured more worms than those in the latter. The blesbok is a new host record for *Longistrongylus curvispiculum, Longistrongylus sabie* and *Nematodirus helvetianus*.

The ectoparasite burdens of the blesbok shot during December 1979 in the Golden Gate and Mountain Zebra Parks are summarized in Table 2.

Of the 7 species of ectoparasites recovered, only *Damalinia crenelata* was present on animals in both reserves.

The mean worm burdens of the blesbok from Badplaas are summarized in Table 3.

A total of 16 nematode and 1 cestode species were recovered from these animals. Every animal was infested with 4th state larvae of *Haemonchus* spp. and *Oesophagostomum* sp. and with adult *Dictyocaulus magnus, Longistrongylus albifrontis* and *Trichostrongylus thomasi*. With few exceptions they also harboured adult *Cooperia hungi, Cooperia yoshidai* and *Impalaia tuberculata*.

Fourth stage larvae of *Haemonchus* spp. and *Oesophagostomum* sp. constituted the major portion of the worm burdens of these 2 genera, while large numbers of 4th stage larvae of *Longistrongylus* sp., *Cooperia* spp. and *Impalaia* sp. were also recovered.

The first 2 animals shot had considerably more *Skrjabinema alata* than any other buck, but no other marked differences in worm burdens were noticeable between the various slaughter dates.

The ectoparasite burdens of 4 blesbok at Badplaas are summarized in Table 4.

TABLE 1 The mean helminth burdens of blesbok in the Golden Gate and Mountain Zebra Parks

No. of blesbok slaughtered	Date slaughtered	Mean numbers of helminths recovered												
			Haemonchus spp.			*Longistrongylus* spp.			*Trichostrongylus* spp.			*Nematodirus* spp.		
		Dictyocaulus magnus	*H. bedfordi*		*H. contortus*		**L. curvispiculum*	**L. sabie*	*T. axei*	*T. colubriformis*	*T. falculatus*		**N. helvetianus*	*N. spathiger*
		Adult	4th	Adult	Adult	4th	Adult	Adult	Adult	Adult	Adult	4th	Adult	Adult
Golden Gate Highlands Park														
2	June 1975	17	0	13	0	0	1 338	100	163	25	25	0	3 375	0
2	Sep. 1975	14	0	70	0	0	115	135	15	0	0	0	75	0
2	March 1976	0	38	163	0	0	50	0	0	0	0	13	175	0
2	Dec. 1979	8	3	61	20	1	169	53	25	0	0	88	203	0
Mountain Zebra National Park														
2	June 1975	5	0	0	0	0	80	0	0	518	0	30	0	520
2	Sep. 1975	1	0	0	0	0	0	135	5	0	0	0	0	30
2	March 1976	0	50	63	0	0	0	0	0	63	0	50	0	63
2	Dec. 1979	0	1	14	0	0	0	0	1	0	13	75	0	60

4th = 4th stage larvae

* New host record

TABLE 2 The ectoparasite burdens of 2 blesbok shot in the Golden Gate Park and 2 blesbok shot in the Mountain Zebra Park during December 1979

Numbers of ectoparasites recovered												
**Gedoelstia cristata*		*Damalinia crenelata*		*Linognathus damaliscus*		**Boophilus decoloratus*		**Hyalomma marginatum turanicum*	*Rhipicephalus evertsi evertsi*		**Rhipicephalus glabroscutatum*	
1st	3rd	N	Adult	N	Adult	L	Adult	Adult	N	Adult	N	Adult
Golden Gate Highlands Park												
3	1	2	0	0	0	0	0	0	0	0	0	0
0	0	22	80	26	6	2	2	0	0	0	0	0
Mountain Zebra National Park												
0	0	0	2	0	0	0	0	4	0	16	0	18
0	0	8	14	0	0	0	0	0	8	4	2	8

1st, 3rd = 1st and 3rd larval stages L = Larvae N =Nymphae

* New host record

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* Triatix: Coopers SA (Pty) Ltd

TABLE 3 The mean helminth burdens of blesbok shot in the Rob Ferreira Nature Reserve during 1978

No. of blesbok slaughtered	Date slaughtered	Mean numbers of helminths recovered																			Other helminths recovered
			Haemonchus spp.					*Trichostrongylus* spp.			*Cooperia* spp.										
		Dictyocaulus magnus		*H. bedfordi*	*H. contortus*	*Longistrongylus albifrontis*			*T. axei*	*T. thomasi*		*C. hungi*	*C. yoshidai*	*Impalaia tuberculata*		*Oesophagostomum columbianum*		*Skrjabinema alata*			
		A	4th	A	A	4th	A	4th	A	A	4th	A	A	4th	A	4th	A	Imm	A		
2	17 May	20	3 323	88	0	223	776	0	1	295	1 067	832	2 588	2 070	7 041	17	2	1 488	3 488		1 animal 2 *Gongylonema* sp.
6	19 June	15	3 835	21	13	410	740	1	1	244	949	1 042	967	1 780	3 821	40	1	104	192		1 animal 328 *T. colubriformis* and 1 510 *T. falculatus;* 1 animal 1 *T. falculatus;* 1 animal 1 *Moniezia* sp.
5	28 June	12	4 270	20	0	146	860	0	70	336	616	1 745	2 730	2 261	6 246	59	2	155	820		
15	19 July	16	5 645	18	42	781	650	1	12	466	1 832	1 162	2 127	2 280	4 851	54	3	93	103		1 animal 1 *Agriostomum equidentatum* and 1 *Trichuris* sp.; 1 animal 1 *Trichuris* sp.

A = Adult
Imm = Immature worms
4th = 4th stage larvae

TABLE 4 The ectoparasite burdens of 4 blesbok shot in the Rob Ferreira Nature Reserve at Badplaas

Date slaughtered	Numbers of ectoparasites recovered															
	**Gedoelstia* sp.			*Kirkioestrus minutus*	*Oestrus macdonaldi*			*Damalinia crenelata*		*Rhipicephalus appendiculatus*			*Rhipicephalus evertsi evertsi*			**Haemaphysalis* sp.
	1st	2nd	3rd	1st	1st	2nd	3rd	Nymphae	Adult	Larvae	Nymphae	Adult	Larvae	Nymphae	Adult	Adult
17 May 1978	138	5	45	2	2	19	43	1	3	6 212	1 354	30	564	336	0	0
17 May 1978	128	6	29	67	0	0	0	0	0	11 846	2 538	27	623	158	0	1
19 June 1978	7	13	21	0	0	0	0	1	0	3 928	1 043	0	329	396	0	0
19 June 1978	67	4	29	2	0	0	0	4	28	2 376	828	4	118	231	1	0

1st, 2nd, 3rd = 1st, 2nd and 3rd stage larvae

* New host record

These animals were infested with the larvae of a *Gedoelstia* sp., the mature 3rd stage larvae of which were very large and differed in certain characteristics from those of *Gedoelstia hässleri* and *Gedoelstia cristata*. They were also infested with larvae of *Kirkioestrus minutus* and *Oestrus macdonaldi*. In addition, they harboured all sages of development of *Rhipicephalus appendiculatus, Rhipicephalus evertsi evertsi* and *D. crenelata*.

The mean helminth and arthropod parasite burdens of the 3 blesbok shot in the Rietvlei Nature Reserve near Pretoria are summarized in Tables 5 & 6.

A total of 7 nematode species, 1 cestode, the larvae of 4 oestrid fly species, a louse and 2 ixodid ticks were recovered from these animals. Of the nematodes *Impalaia nudicollis* constituted the major portion of the burden of 2 of the blesbok, while the same 2 animals also had fairly large burdens of *C. yoshidai*.

No 1st stage *Gedoelstia* sp. larvae were seen in the eyes or recovered from the brains, cranial cavities, hearts or lungs of any of the blesbok, but they were recovered from the nasal passages, which also harboured 2nd and 3rd stage *G. cristata* larvae. The nasal passages of the 3 animals also contained 1st stage larvae of *K. minutus* but no 1st stage *Oestrus* spp. larvae. These, however, were recovered from the lungs of 2 animals.

The mean helminth burdens of the bontebok are summarized in Table 7.

The lungs and the abomasal and intestinal mucosae of only the 8 animals shot during December 1979 were processed for helminth recovery. All these animals were infested with *D. magnus* and *Protostrongylus capensis;* and 1 also harboured *Pneumostrongylus cornigerus*. The majority of these animals also had large burdens of 4th stage larvae of *Longistrongylus* spp. and *N. spathiger*. The lungs of the animals shot during September 1975 were examined for the presence of lungworms. All were infested with *P. capensis,* 2 with *P. cornigerus* and 1 with *D. magnus*.

A total of 9 gastro-intestinal nematode species were recovered from the bontebok. Of these *Cooperia curticei* was present in the animals shot during 1975 and 1976 but not during 1979. The bontebok is a new host record for *Longistrongylus curvispiculum, Longistrongylus namaquensis, Cooperia curticei, Agriostomum equidentatum* and *Trichostrongylus pietersi*.

The ectoparasite burdens of the 8 bontebok shot during December 1979 are summarized in Table 8.

	Haemonchus spp.		*Trichostrongylus axei*	*Cooperia yosidai*		*Impalaia nudicollis*		*Skrjabinema alata*		*Trichuris* sp.	*Avitellina* sp.
	H. bedfordi	*H. contortus*									
4th	Adult	Adult	Adult	4th	Adult	4th	Adult	Imm	Adult	Adult	Scolices
70	0	75	70	75	975	280	0	100	225	0	0
75	6	5	10	370	1 925	770	5 750	50	325	1	1
1 055	26	24	50	970	4 750	1 375	19 275	0	0	0	0

Gedoelstia cristata			*Kirkioestrus minutus*	*Oestrus* spp.			*O. variolosus*	*Damalinia crenelata*		*Boophilus* sp.	*Rhipicephalus evertsi evertsi*		
					O. macdonaldi								
1st	2nd	3rd	1st	1st	2nd	3rd	3rd	Nymphae	Adults	Larvae	Larvae	Nymphae	Adults
55	12	2	90	0	2	7	0	1 148	688	8	356	144	2
129	11	9	147	3	15	30	0	6 260	4 256	0	78	30	0
31	20	17	94	8	14	23	1	128	88	0	360	192	0

1st, 2nd, 3rd = 1st, 2nd and 3rd stage larvae

TABLE 7 The mean helminth burdens of bontebok in the Bontebok National Park

		Mean numbers of helminths recovered											Other helminths recovered
						Longistrongylus spp.							
No. of bontebok slaughtered	Month slaughtered	*Dictyocaulus magnus*	*Protostrongylus capensis*	*Haemonchus contortus*			**L. curvispiculum*	**L. namaquensis*	*Trichostrongylus axei*	**Cooperia curticei*	*Nematodirus spathiger*		
		A	A	4th	A	4th	A	A	A	A	4th	A	
8	June 1975	—	—	0	0	0	3 903	584	153	38	44	1 459	
9	Sept 1975	—	Positive	0	0	7	1 177	169	72	17	35	1 125	1 animal positive *Dictyocaulus magnus;* 2 animals positive *Pneumostrongylus cornigerus;* 1 animal 2 **Agriostomum equidentatum;* 1 animal 4 390 **Trichostrongylus pietersi* and 4 390 *Trichostrongylus rugatus*.
6	March 1976	—	—	0	0	175	2 817	363	8	29	165	483	
8	Dec 1979	29	66	17	3	7 994	4 870	73	225	0	7 464	8 606	1 animal 4 *Pneumostrongylus cornigerus*.

4th = 4th stage larvae
A = Adult
* = New host record

TABLE 8 The ectoparasite burdens of 8 bontebok shot in the Bontebok National Park during December 1979

Numbers of ectoparasites recovered										
**Gedoelstia* sp.			*Damalinia* sp.		*Ixodes* sp.	**I. pilosus*	*Rhipicephalus* sp.	**R. nitens*	**Amblyomma marmoreum*
1st	2nd	3rd	Nymphae	Adult	Nymphae	Adult	Nymphae	Adult	Adult
59	26	79	12	22	0	0	5	318	0
81	36	15	4	0	2	1	5	343	0
70	25	42	0	0	6	0	7	79	0
111	19	61	0	10	0	0	2	366	0
42	16	41	0	8	0	0	8	18	1
44	25	66	0	6	0	3	4	152	0
43	31	23	0	0	0	2	2	73	0
83	28	38	0	12	7	4	4	83	0

1st, 2nd, 3rd = 1st, 2nd and 3rd larval stages
* New host record

All the buck were infested with the larvae of a *Gedoelstia* sp., the mature 3rd stage larvae of which were very large and similar in appearance to those recovered from the blesbok at Badplaas. A large proportion of the 1st stage larvae of this fly was recovered from the right ventricles of the hearts of these animals but no larvae were found in the cranial cavities. All were also infested with adult *Rhipicephalus nitens*.

DISCUSSION

A total of 21 nematode and 2 cestode species were recovered from blesbok in the 4 parks. Of these only *Haemonchus bedfordi* and *Trichostrongylus axei* were present in animals from each region. The larvae of 5 oestrid flies and the immature and/or adult stages of 6 ixodid ticks and 2 lice were also recovered. Of these only *D. crenelata* was present on animals in each of the 4 parks.

The bontebok harboured 12 nematode species, the larvae of an oestrid fly, a biting louse and 3 ixodid tick species. Of these *D. magnus, L. curvispiculum, T. axei, N. spathiger,* and the larvae of a large *Gedoelstia* species were also recovered from some of the blesbok.

Golden Gate and Mountain Zebra Parks

The small number of nematodes recovered from blesbok in both these parks is probably largely due to the low stocking density. In addition, the particularly small numbers present in the antelope in the Mountain Zebra Park can be ascribed to the fact that this is a semi-arid region with a mean annual rainfall of 398 mm.

The majority of species recovered had previously been recorded from blesbok (Horak, 1978 a) or were present in the animals slaughtered at Badplaas. *L. curvispiculum,* however, had not previously been reported in blesbok. This nematode was originally described from Grant's gazelle (Gibbons, 1973) and has also been recovered from several wild ruminants in East Africa (Gibbons, 1977).

But for its presence in the blesbok in the Golden Gate Park and in springbok near Krugersdorp in the western Transvaal (Horak, Meltzer & De Vos, 1982), *N. helvetianus* has apparently not previously been recovered from wild ruminants.

Only 1 of the 2 blesbok examined in the Golden Gate Park was infested with larvae of *G. cristata*. Four of an additional group of 5 blesbok examined in the park at the same time were infested but harboured a total of only 23 larvae.

Linognathus damaliscus was originally described from material obtained from both bontebok, which is the type-host, and blesbok (Bedford, 1936), and the *Linognathus* sp. recovered from 1 of the blesbok at Golden Gate, has provisionally been assigned to this species. Ledger (1980), however, suggests that a detailed study of adequate material may indicate that the species on blesbok differ from those on bontebok and could be a separate species as proposed by Fiedler & Stampa (1956).

Few ticks were recovered from the animals in either of the reserves, the difference in the species recovered from the 2 localities being a reflection of the differences in their geographical distributions (Howell, Walker & Nevill, 1978).

Badplaas

The blesbok at Badplaas harboured a greater number and a considerably greater variety of helminth parasites than the blesbok at Lunsklip or near Pretoria (Horak, 1978 a). Although other buck ran with the blesbok at each of those localities, the smaller area of the reserve at Badplaas, coupled with the high stocking rate, probably accounted for the larger worm burdens and greater number of species recovered.

H. bedfordi was recently recovered from blesbok for the first time (Horak, 1978 a) and, although originally described from blue wildebeest and African buffalo by Le Roux (1929), it has been recovered from numerous antelope species (Round, 1968; Gibbons, 1979). It thus appears not to be particularly host specific.

T. thomasi was originally described from impala (Mönnig, 1932, 1933) and had apparently not been encountered in any other species. However, it has recently been recovered from springbok (Horak *et al.*, 1982) and blue wildebeest (Horak, unpublished data, 1978), and the fact that all the blesbok at Badplaas were infested indicates a considerably wider host range than was previously thought. Male worms of *C. hungi* were originally described from waterbuck (Mönnig, 1931) and females from tsessebe (Mönnig, 1932) and numerous other antelope species are also infested with this worm (Round, 1968). Impala examined at Boekenhout (Horak, 1978 b) and at Pafuri (Horak, 1980 b) also harboured *C. hungi,* and it is probable that, if *T. thomasi* and *C. hungi* are not specific parasites of blesbok, the presence of a herd of 122 impala in the confined space of the reserve at Badplaas, and presumably harbouring these parasites, ensured that the blesbok became infested.

Until recently *C. yoshidai* had been recovered only from reedbuck (Mönnig, 1939) and mountain reedbuck (Baker & Boomker, 1973). It has subsequently been found in blesbok (Evans, 1978), however, and its presence in virtually every animal at Badplaas indicates that it is well-adapted to this host.

Mönnig (1932) recovered *Oesophagostomum columbianum* from blesbok artificially infested with larvae of this worm. Its presence in naturally infested blesbok has been recorded, however, by Fourie (1951) and Ortlepp

(1961), and its recovery from a large number of African antelope species (Round, 1968) seems to indicate an old association.

The recovery of a single *Agriostomum equidentatum* from 1 of the 28 blesbok examined indicates that its presence is probably accidental and a result of the fact that 93 springbok, the antelope from which it was originally described (Mönnig, 1929), grazed the reserve with the blesbok.

The recovery of *S. alata* from blesbok at Lunsklip and in the Rietvlei Nature Reserve near Pretoria (Horak, 1978 a) and Badplaas and Rietvlei in the present survey, infers that it should be considered a parasite of blesbok, although it was originally described from sheep (Mönnig, 1932).

The large proportion of early 4th stage larvae of *Haemonchus* spp., *Longistrongylus* sp., *Cooperia* spp. and *Impalaia* sp. recovered is probably because the animals were all culled during the period May–July (winter) and that these nematodes were overwintering in the blesbok as arrested 4th stage larvae.

The fairly substantial numbers of adult *L. albifrontis, Cooperia* spp. and *I. tuberculata* recovered from the same animals are probably the result of the warm, frost-free winters experienced at Badplaas, which makes survival outside the host possible and removes the necessity for complete inhibition of development. Even these conditions were probably not favourable for the development and survival of the free-living stages of *Haemonchus* spp. and arrest in development was virtually complete. It seems likely that the same phenomenon accounted also for the large proportion of 4th stage larvae of *Oesophagostomum* sp. recovered.

The mature 3rd stage larvae of the *Gedoelstia* sp. recovered from blesbok at Badplaas gave rise to adult flies considerably larger than adult *G. cristata* or *G. hässleri*. Basson, Zumpt & Bauristhene (1963) have described a giant variety of *G. cristata,* which they assumed to be a hybrid between *G. hässleri* and *G. cristata*. As neither *G. hässleri* nor *G. cristata* larvae were recovered from the blesbok at Badplaas, it can be assumed that no adult flies of these species were present. Hence, the larvae recovered could hardly be a hybrid between these 2 flies and probably belong to a valid separate species.

K. minutus is a parasite of blue wildebeest (Zumpt, 1965) and it has been suggested by Horak, Boomker & De Vos (1980) that, as only 1st stage larvae were recovered from the blesbok at Badplaas, it may not be capable of completing its parasitic life cycle in this host. *O. macdonaldi* has been recovered from blesbok near Pretoria and near Lunsklip in the northern Transvaal (Horak & Butt, 1977). Third stage larvae of this fly appear to be present only from May–September (Horak & Butt, 1977).

The large burdens of immature *R. appendiculatus* present on the blesbok were probably due to 3 factors. Firstly, the time of the year, as peak immature activity occurs between March and September (Londt, Horak & De Villiers, 1979); secondly, the high stocking density in the reserve which thus supplies an abundance of hosts for all stages of development and, thirdly, the presence of eland, which are good hosts for adult ticks and which in turn give rise to large immature populations.

The large numbers of immature *R. evertsi evertsi* can also be ascribed to the 1st 2 of the above-mentioned 3 factors and to the presence of zebras in the reserve, as these animals are good hosts of the adults of this tick (Horak, unpublished data, 1980).

Rietvlei Reserve

The parasite burdens of the blesbok in this reserve are of interest, not only because they can be compared with those of the blesbok in other reserves, but also because they can be compared with those of 4 blesbok shot almost exactly 9 years previously in the same reserve (Horak & Butt, 1977; Horak, 1978 a).

In contrast to the blesbok at Badplaas, which harboured *I. tuberculata,* these animals were infested with *I. nudicollis,* a parasite also recovered from blesbok in the Percy Fyfe Nature Reserve in the northern Transvaal (Horak, 1978 a). Each of the 3 blesbok from the Rietvlei Reserve also harboured *C. yoshidai,* a parasite recovered from nearly all the animals at Badplaas but not recovered from the 4 blesbok shot 9 years previously in the Rietvlei Reserve (Horak, 1978 a).

Horak & Butt (1977) also recovered large numbers of 1st stage larvae (which they assumed to be *Oestrus* spp.), from the nasal passages of those 4 blesbok. One of those animals also harboured *Oestrus* spp. larvae in its lungs. At the time, the 1st stage larvae of *K. minutus,* which have only recently been described (Horak *et al.*, 1980), were not known. However, because of the findings in the 3 blesbok in the present survey in the Rietvlei Reserve, the 1st stage larvae recovered from the nasal passages of the previously examined blesbok were re-examined and found to be 1st stage larvae of *K. minutus*. Unfortunately, the larvae recovered from the lungs of 1 of those animals had been lost, and thus it could not be determined if they were indeed *Oestrus* sp. larvae.

It was also suggested by Horak & Butt (1977) that 3rd stage larvae of *O. macdonaldi* were present in blesbok only during the period May–Sepember, a suggestion now supported by the fact that 1 of the blesbok slaughtered at Badplaas during May 1978 harboured these larvae, as did the 3 blesbok now examined in the Rietvlei Reserve. They also suggested that, if blesbok in the Rietvlei Reserve were examined at other times of the year, they might be found to harbour *Oestrus variolosus* as well. The recovery of a single 3rd stage larva of *O. variolosus* from 1 of the animals now examined and from 3 black wildebeest culled a little later in the Rietvlei Reserve confirms that this parasite does occur in this reserve.

Each of the 3 blesbok was infested with larvae of *G. cristata,* and on re-examination of the larvae recovered from the 4 blesbok previously examined at Rietvlei it was found that all the larvae previously identified as *G. hässleri* were in fact also *G. cristata* larvae.

The presence of substantial numers of immature *R. evertsi evertsi* in the ears of the blesbok was probably due to the presence of zebras in the Rietvlei Reserve.

Bontebok Park

Although *D. magnus* was originally described from the closely related blesbok (Mönnig, 1932), it seems equally well adapted to bontebok. It would appear, however, that this parasite was not introduced into the present Bontebok Park with the bontebok when they were transferred thither from the old Bontebok Park near Bredasdorp during 1960, a fact also mentioned by Verster *et al.* (1975). This observation is supported by the fact that no *D. magnus* were recovered from the animals in the original park before they were transferred (Ortlepp, 1962). Springbok, which are also good hosts of *D. magnus,* were subsequently introduced into the new park (Penzhorn, 1971) and the infestation probably came with them. Both *Pneumostrongylus cornigerus* and *Protostrongylus capensis* were originally described from bontebok (Ortlepp, 1962).

Longistrongylus namaquensis was originally described from the abomasum of a sheep (Ortlepp, 1963), but has subsequently been found in springbok in the Bontebok National Park (Horak *et al.*, 1982). It may well prove to be a parasite of wild ruminants in common with the other members of this genus (Gibbons, 1977).

More than 60% of the total *Longistrongylus* spp. burdens of the animals culled during December 1979, the abomasal mucosae of which had been digested, were in the 4th stage of larval development. This can probably be ascribed to arrested development ensuring the survival of the nematode in a stable internal environment during a time when the external dry and hot conditions of summer in the western Cape Province are unsuitable for survival of the free-living stages. Unfortunately this statement cannot be substantiated from a comparison with the burdens of the animals slaughtered during June and September 1975 and March 1976. The abomasal mucosae of these animals had not been digested and, consequently, their burdens of *Longistrongylus* spp. larvae cannot be considered complete, as very large numbers of 4th stage larvae of this genus are frequently present in the mucosa of the abomasum.

The presence of large numbers of adult *N. spathiger* in adult bontebok is worth noting. In a helminth survey conducted in sheep in the Karoo, Viljoen (1969) found that once the sheep reached 12–15 months of age, regardless of the season of the year, fewer *N. spathiger* became adult. He thought that this was probably a manifestation of age resistance similar to that found against this and other species of the genus (Brunsdon, 1962 a). Whether the large proportion of adult *N. spathiger* found in the present survey was indicative of a well-adapted, definitive host/parasite relationship (Horak, 1980 b) or of a decrease in host resistance brought about by inadequate nutrition (Brunsdon, 1962 b) or by the presence of large burdens of other parasites, could not be determined within the limits of this survey.

Few *N. spathiger* larvae were recovered from the digested intestinal mucosae of the animals slaughtered during December 1979. Hence the larval burdens of this species in the animals culled during 1975 and 1976 can be taken as a reasonably accurate reflection of the actual number of larvae present. From these observations it would appear that a degree of arrested development in the 4th larval stage was present during December 1979.

Verster *et al.* (1975) recovered fairly large numbers of *Ostertagia hamata* and *N. spathiger* from the bontebok they examined during 1973. Although *O. hamata* was absent in all the bontebok examined in the present survey, *N. spathiger* was recovered in large numbers.

The recovery of larvae of a very large *Gedoelstia* sp. from the bontebok in the absence of larvae of either *G. cristata* or *G. hässleri* is further support for our contention that this is a valid, separate species. The fairly large numbers of 1st stage larvae found in the hearts of the antelope, while none were present around the brains, suggests that the larvae of these flies follow a migratory route from the cornea to the blood vessels, heart, lungs, trachea, pharynx and nasal cavity in preference to the route via the cornea, optic nerve, dura mater and foramina of the cribriform plate to the nasal cavity (Horak & Butt, 1977).

The *Damalinia* sp. recovered from the bontebok has only been identified to generic level, as it is probable that this is an unnamed new species (Ledger, 1980).

The large numbers of adult *R. nitens* recovered from the bontebok indicate that they are efficient hosts of this tick, which has a geographical distribution limited to the south-western Cape Province (Morel, 1969). The single adult *Amblyomma marmoreum* recovered is an indication of the presence in the park of a large number of tortoises, which this tick parasitizes (Hoogstraal, 1956).

ACKNOWLEDGEMENTS

We should like to thank the National Parks Board for placing the blesbok in the Golden Gate Highlands Park and the Mountain Zebra National Park and the bontebok in the Bontebok National Park at our disposal. The Board of Public Resorts also kindly made available the blesbok in the Rob Ferreira Nature Reserve. Sentrachem (Pty) Limited and Hoechst Pharmaceuticals (Pty) Limited furnished financial support for the survey at the Rob Ferreira Nature Reserve and Dr W. M. O'Donovan arranged the culling of the animals at this venue.

This research was also funded by the University of Pretoria and the Council for Scientific and Industrial Research.

The assistance of Mrs Evelyn L. Visser and Messrs J. V. Badenhorst, B. D. de Klerk, I. L. de Villiers, N. H. Jonker, P. C. Pieterse and H. Scott with processing the necropsies is gratefully acknowledged.

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Printed by and obtainable from the Government Printer, Bosman Street, Private Bag X85, Pretoria, 0001

Onderstepoort J. vet. Res. 55, 145–152 (1988)

PARASITES OF DOMESTIC AND WILD ANIMALS IN SOUTH AFRICA. XXIII. HELMINTH AND ARTHROPOD PARASITES OF WARTHOGS, *PHACOCHOERUS AETHIOPICUS,* IN THE EASTERN TRANSVAAL LOWVELD

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ABSTRACT

HORAK, I. G., BOOMKER, J., DE VOS, V. & POTGIETER, F. T., 1988. Parasites of domestic and wild animals in South Africa. XXIII. Helminth and arthropod parasites of warthogs, *Phacochoerus aethiopicus*, in the eastern Transvaal Lowveld. *Onderstepoort Journal of Veterinary Research*, 55, 145–152 (1988).

A total of 69 warthogs, *Phacochoerus aethiopicus,* were collected from 4 localities within the Kruger National Park, eastern Transvaal Lowveld. These animals harboured 16 nematode species, 2 trematodes, 1 or 2 species of adult cestodes and the larval stages of 4 cestodes. No pattern of seasonal abundance could be determined for any of the helminths.

The warthogs were also infested with 3 flea species, 1 louse species, 8 ixodid tick species. 1 argasid tick and the nymphae of a pentastomid. The seasonal abundance of fleas of the genus *Echidnophaga,* of the sucking louse *Haematopinus phacochoeri* and the ixodid ticks *Amblyomma hebraeum, Rhipicephalus appendiculatus, Rhipicephalus simus* and *Rhipicephalus zambeziensis* was determined.

INTRODUCTION

The prevalence of several endo- and ectoparasites of warthogs, *Phacochoerus aethiopicus,* in South West Africa/Namibia has recently been reported (Horak, Biggs, Hanssen & Hanssen, 1983). The warthogs were infested with 9 nematode species, 1 or 2 cestode species, 6 species of ixodid ticks, 1 argasid tick species, a flea and a louse species and the larvae of a dipteran fly. Only the spirurid stomach worm *Physocephalus sexalatus* and the sucking louse *Haematopinus phacochoeri* exhibited clear patterns of seasonal abundance.

The present paper describes a similar survey conducted on warthogs in the Kruger National Park in the eastern Transvaal Lowveld.

MATERIALS AND METHODS

Survey region

Warthogs were collected from 4 localities within the Kruger National Park. These were Skukuza (24° 58′ S, 31° 36′ E; Alt. 262 m), Crocodile Bridge (25° 22′ S, 31° 54′ E; Alt. 217 m) and Lower Sabie (25° 07′ S, 31° 55′ E; Alt. 180 m) all situated in a vegetation zone classified as Lowveld; and Pafuri (23° 27′ S, 31° 19′ E; Alt. 305 m) where the vegetation is classified as Mixed Bushveld (Acocks, 1975). Gertenbach (1983) has identified 35 landscape types within the Park. According to his classification Skukuza lies within a region classified as Thickets of the Sabie and Crocodile Rivers; Crocodile Bridge and Lower Sabie in *Sclerocarya caffra/Acacia nigrescens* Savanna; and Pafuri within the Limpopo/Levumbu Flood plains.

Survey animals

With the exception of June 1980, when 1 extra warthog was shot, 1 animal from the most recent litter of piglets (which are generally born in November or December) and 1 older animal were shot at Skukuza each month from January 1980 to January 1981. Except for 1 animal of approximately 11 months of age, 2 warthogs of 12 months or older were shot each month at Crocodile Bridge over the same period. A total of 53 warthogs were collected at the 2 localities in this manner.

In addition 5 warthogs were shot at Pafuri during July 1980 and 2 during October 1981; 2 were shot at Lower Sabie during July 1980, 3 were shot at Skukuza during October and November 1982; and 4 animals were shot at Crocodile Bridge during November 1982.

Parasite recovery

The carcasses of the warthogs shot at Skukuza, Crocodile Bridge and Lower Sabie were transported to the laboratory at Skukuza where they were processed for parasite recovery. Those shot near Pafuri were transported to a nearby field laboratory where they were similarly processed.

At the laboratories unattached fleas and ticks were collected and stored in 70 % alcohol. Thereafter the carcasses were skinned and the skins were processed for ectoparasite recovery as described by Horak, De Vos & De Klerk (1984).

Numerous fleas being deeply imbedded in the skin, were not loosened by the parasite recovery process, and could not be removed with forceps without damage. Consequently, they were counted *in situ* and a small number removed for identification. This procedure, however, made it impossible to determine the exact numbers of the stick-tight fleas *Echidnophaga inexpectata* and *Echidnophaga larina* separately.

The nasal passages and paranasal sinuses of the first 13 warthogs shot were cut open and examined for oestrid larvae as described by Horak (1977). When these contained no larvae no further nasal passages were examined.

The carcasses were eviscerated and all visible cestode cysts collected. The lungs, the livers and the gastro-intestinal tracts were processed for helminth recovery as described by Horak, De Vos & Brown (1983).

Parasite counts

The lung and liver washings were examined *in toto* under a stereoscopic microscope for helminths as were several of the digests of the gastro-intestinal mucosae. Representative samples of the remaining digests as well as of all the gastro-intestinal ingesta were examined under the same microscope. The remains of the gastro-intenstinal contents were examined macroscopically for large nematodes and for cestodes in a flat-bottomed tray.

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Received 4 May 1988—Editor

TABLE 1 The helminth parasite recovered from 52 warthogs in the Kruger National Park

Helminth species	Total numbers of helminths recovered				Number of warthogs infested
	3rd stage	4th stage	Adult	Total	
Ascaris phacochoeri	25	2	35	62	16
Impalaia tuberculata	0	236	566	802	11
Murshidia spp.	0	4 411	—	4 411	17
Murshidia hamata	—	—	87 506	87 506	39
Murshidia pugnicaudata	—	—	18 706	18 706	35
Oesophagostomum spp.	0	2 256	—	2 256	17
Oesophagostomum mocambiquei	—	—	52 291	52 291	43
Oesophagostomum mwanzae	—	—	5 185	5 185	26
Physocephalus sexalatus	196	36	666	898	25
Probstmayria vivipara	—	Millions	—	—	52
Strongyloides sp.	0	0	116	116	3
Trichostrongylus spp.	0	139	—	139	8
Trichostrongylus falculatus	—	—	50	50	1
Trichostrongylus instabilis	—	—	793	793	4
Trichostrongylus thomasi	—	—	7 892	7 892	39
Trichuris sp.	0	10	0	10	1
Schistosoma sp.	—	—	15	15	1
Moniezia/Paramoniezia sp.	—	—	58*	58	11
Echinococcus sp.		Cysts			8
Taenia crocutae		Cysticerci			4
Taenia hyaenae		Cysticerci			3
Taenia regis		Cysticerci			15

* Scolices

TABLE 2 The arthropod parasites recovered from 51 warthogs in the Kruger National Park

Arthropod species	Total numbers of arthropods recovered					Number of warthogs infested
Fleas	Adults				Total	
Echidnophaga inexpectata/larina	12 932				12 932	46
Moeopsylla sjoestedti	143				143	23
Lice	Nymphae		Adults		Total	
Haematopinus phacochoeri	2 902		533		3 435	34
Ixodid ticks	Larvae	Nymphae	Males	Females	Total	
Amblyomma hebraeum	3 777	3 014	1 028*	348* (24)	8 167	51
Boophilus decoloratus	112	63	39	24 (0)	238	29
Hyalomma truncatum	0	0	7	3 (0)	10	7
Rhipicephalus appendiculatus	—	1 537	—	—	1 537	23
Rhipicephalus appendiculatus/zambeziensis	904	—	27	10 (0)	941	20
Rhipicephalus evertsi evertsi	8	9	0	0	17	11
Rhipicephalus simus	0	0	387	173 (5)	560	27
Rhipicephalus zambeziensis	—	526	—	—	526	19
Argasid ticks	Larvae	Nymphae	Adults		Total	
Ornithodoros porcinus porcinus	0	374	0		374	27
Pentastomids		Nymphae			Total	
Linguatula nuttalli		91			91	18

* Including *A. hebraeum* 525 males, 128 females collected from a single male adult warthog

() Number of maturing female ticks, i.e. the idiosoma of *A. hebraeum* >9,0 mm; *B. decoloratus* >4,0 mm; *H. truncatum* >7,5 mm; *R. appendiculatus/zambeziensis* >5,0 mm, *R. simus* >6,0 mm

The cestodes were not specifically identified but belonged to the genera *Moniezia* or *Paramoniezia*. Ticks, lice and unattached fleas were counted by the methods described by Horak, Potgieter, Walker, De Vos & Boomker (1983). The larvae and adults of *Rhipicephalus appendiculatus* and *Rhipicephalus zambeziensis* were not separated and these were lumped as *Rhipicephalus appendiculatus/zambeziensis*. The length of the idiosoma of adult engorging female ticks of all species was measured. The *Ornithodoros* ticks recovered from the warthogs have been assigned to *Ornithodoros porcinus porcinus* on host preference as suggested by Walton (1962).

Blood parasites

Blood smears were prepared as soon as possible after death. Impression smears of the spleen and lymphnodes were made during necropsy. Smears were made from 18 animals in 3 localities: 8 each from Skukuza and Crocodile Bridge and 2 from Pafuri. All the smears were fixed in methanol, stained in 10 % Giemsa stain for 35 min and examined in immersion oil under 1 000 × magnification.

Climatic data

Mean monthly minimum and maximum atmospheric temperatures and monthly rainfall were recorded at Skukuza.

RESULTS

Helminths

The total numbers of helminths recovered from 52 warthogs slaughtered at monthly intervals at Skukuza and Crocodile Bridge are summarized in Table 1 (the ingesta of 1 animal were mislaid).

Thirteen nematode species, 1 trematode, 1 or 2 cestode species and the larval stages of 4 cestodes were recovered. *Probstmayria vivipara, Murshidia hamata* and *Oesophagostomum mocambiquei* were the most abundant helminths recovered. A large proportion of the total numbers of the latter 2 worms came from a single animal, which harboured 5 000 adult *O. mocambiquei* and 38 200 adult *M. hamata*.

All the *Impalaia tuberculata* rococvered from the warthogs were considerably smaller than normal and the males' spicules were markedly reduced in length.

A young warthog, 1 month of age, was infested with *Strongyloides* sp. This was the only helminth recovered from this animal. No *Strongyloides* sp. were recovered from the piglets of 2 or 3 months of age, but the 4-month-old animal and an adult animal from Crocodile Bridge were also infested. No other warthogs harboured this parasite.

Ascaris phacochoeri, O. mocambiquei, P. sexalatus, Trichostrongylus thomasi and *Trichostrongylus instabilis* and *Moniezia/Paramoniezia* sp. were recovered from the 2-month-old warthog. *M. hamata* and *Murshidia pugnicaudata* were first encountered when the warthogs were 6 months of age and *Oesophagostomum mwanzae* in a 7-month-old animal.

No pattern of seasonal abundance could be determined for any of the helminths.

The animals shot at Skukuza and Crocodile Bridge during October and November 1982 harboured the same parasites as those examined 2 years earlier at these localities and in addition 1 harboured 28 adult *Haemonchus krugeri* and another 100 adult *Oesophagostomum santos-diasi*. Those examined at Pafuri harboured only *A. phacochoeri, I. tuberculata, M. hamata, M. pugnicaudata, O. mocambiquei, P. vivipara* and *Moniezia/Paramoniezia* sp. One was also infested with 2 *Gastrodiscus aegyptiacus*. The 2 arthogs examined at Lower Sabie harboured only *M. hamata, M. pugnicaudata, O. mocambiquei* and *T. thomasi*.

Two of the warthogs had unidentified adult filarid nematodes in the lymphatic vessels adjacent to peripheral and visceral lymph nodes and 13 had microfilariae in the lymph nodes and the circulating blood (Palmieri, Pletcher, De Vos & Boomker, 1985).

Arthropods

The total numbers of ectoparasites recovered from 51 warthogs slaughtered at monthly intervals at Skukuza and Crocodile Bridge are summarized in Table 2 (no preservative had been added to the skin scrubbings of 2 animals and these could not be examined).

These animals harboured 3 flea species, a louse species, 7 ixodid tick species, 1 argasid tick and the nymphae of a pentastomid. All the animals were infested with *Amblyomma hebraeum* and the majority with 1 or both *Echidnophaga* species.

TABLE 3 A comparison of the burdens of *Amblyomma hebraeum* of warthogs examined during a normal and a dry year using the Mann-Whitney U-test

Months examined	Rainfall (mm) Feb–Nov	Number of warthogs examined (sex rations)	Mean numbers (range) of *A. hebraeum* recovered								
			Larvae	U (sign)	Nymphae	U (sign)	Males	U (sign)	Females	U (sign)	Total
Oct/Nov 1980	414,5	8 (1 male: 7 females)*	18,6 (0–35)		24,4 (11–44)		7,6 (2–28)		3,3 (1–11)		53,9
Oct/Nov 1982	175,4	7 (5 males: 2 females)*	416,0 (56–1233)	0 (<0,001)	259,7 (27–858)	8 (<0,01)	203,1 (12–75)	8 (<0,01)	88,6 (5–308)	16 (=0,052)	967,4

* There is no statistical difference between the burdens of the male and female warthogs
(sign) = (significance)

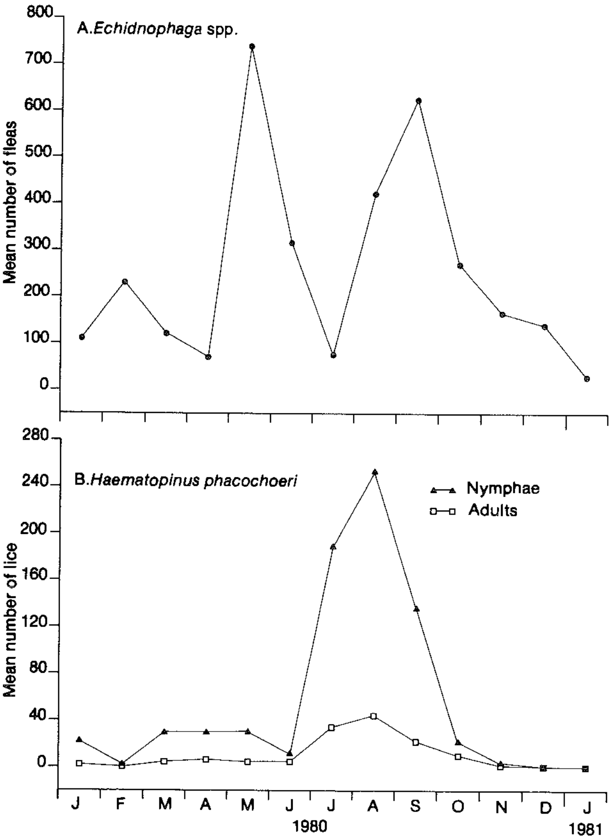

FIG. 1 The seasonal abundance of
A. *Echidnophaga* spp. and
B. *Haematopinus phacochoeri*
on warthogs in the Kruger National Park

At 1 month of age a warthog piglet had acquired infestation with *H. phacochoeri* and with 3 ixodid tick species. At 2 months of age a piglet harboured *H. phacochoeri, Echidnophaga* spp., 4 ixodid tick species and *Ornithodoros porcinus porcinus*. The piglets were 5 months old before the nymphae of *Linguatula nuttalli* were recovered from 1 of them.

The numbers of *A. hebraeum* larvae, nymphae and males recovered from the animals shot at Skukuza and Crocodile Bridge in October and Novemvber 1982, during a severe drought, were significantly greater (P<0,01) than those recovered from the animals shot at the same sites during the same months in 1980, a year of normal rainfall. The tick burdens of the 2 groups of animals are summarized in Table 3.

With the exception of adult *Rhipicephalus kochi,* which were recovered in small numbers from 4 out of the 7 warthogs shot at Pafuri, the animals from Pafuri and those from Lower Sabie were infested with the same parasites as those shot at Skukuza and Crocodile Bridge.

Some of the arthropod parasites exhibited distinct patterns of seasonal abundance. These are graphically illustrated in Fig. 1 & 2.

Peak burdens of the 2 *Echidnophaga* species were present during May and September. Peak numbers of *H. phacochoeri* were recovered from July to September.

The larvae of *A. hebraeum* peaked from February to May, the nymphae during May and during August and September, while peak adult burdens were recovered from January to March and during September 1980 and January 1981. The larvae of *R. appendiculatus/zambeziensis* were recovered in the greatest numbers from April to June and the adults from March to May. The nymphae of both *R. appendiculatus* and *R. zambeziensis*

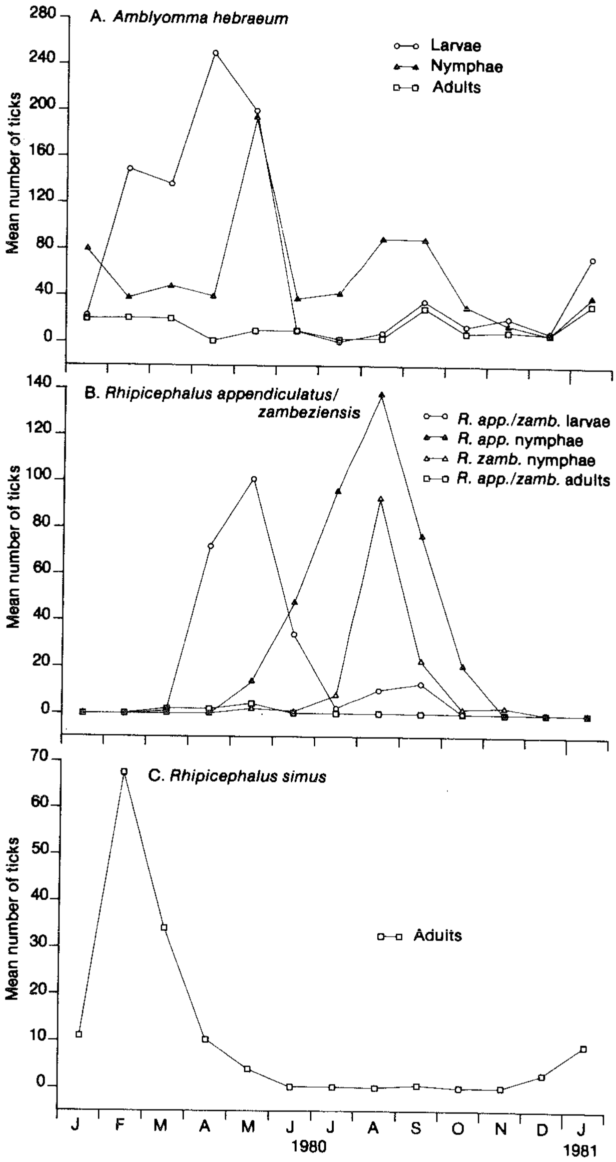

FIG. 2 The seasonal abundance of
A. *Amblyomma hebraeum* (excluding 1 animal with an exceptionally large adult burden)
B. *Rhipicephalus appendiculatus/zambeziensis* and
C. *Rhipicephalus simus*
on warthogs in the Kruger National Park

peaked during August. Peak burdens of adult *Rhipicephalus simus* were present during February.

Blood parasites

All smears examined were negative for blood parasites.

Climate

The mean monthly atmospheric temperatures and total monthly rainfall at Skukuza for the period January 1980 to January 1981 are graphically illustrated in Fig. 3.

The highest maximum temperatures were recorded during January to April and December 1980 and during January 1981, and the lowest minimum temperatures during June and July 1980. Rain fell mainly during January and February 1980 and during November 1980 to January 1981. Total annual rainfall for 1980 at Skukuza was 660,0 mm. Total annual rainfall during 1982 (the year of the severe drought) was 437,2 mm, 202,5 mm of which fell during January 1982 and 59,3 mm during December 1982, leaving 175,4 mm for the remaining 10 months.

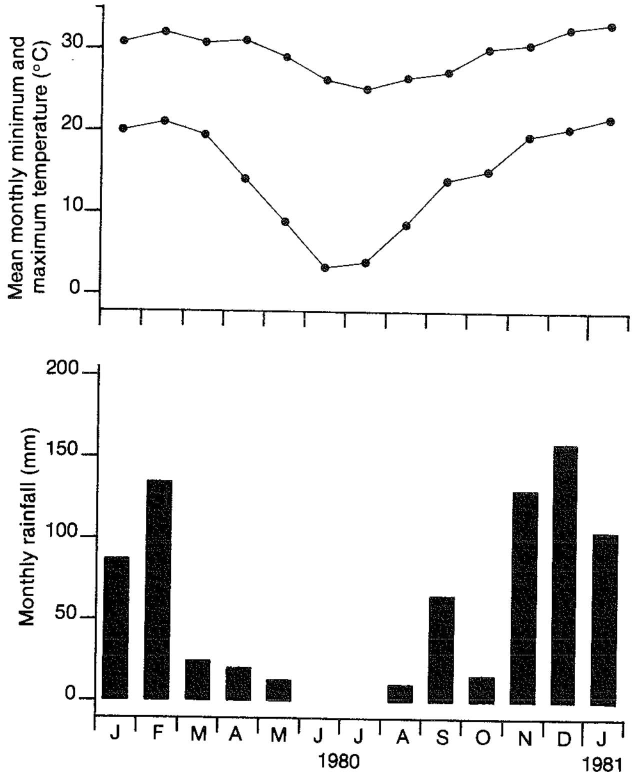

FIG. 3 Monthly mean minimum and maximum atmospheric temperatures and monthly rainfall at Skukuza from January 1980 to January 1981

Comment: The 60 year mean rainfall for February to November at Skukuza is 375,1 mm (Gertenbach, unpublished data, 1981). If the annual rainfall is calculated per season, i.e. from 1 July to 30 June (Gertenbach, 1980), the total for 1982/83 (275,6 mm) is the lowest ever recorded at Skukuza since records were started in 1919 (Gertenbach, unpublished data, 1985).

DISCUSSION

The warthogs examined in Namibia by Horak, Biggs, Hanssen & Hanssen (1983) harboured at least 10 helminth species and 10 arthropod species. Those examined in the Kruger National Park were infested with at least 19 helminth species (plus the larval stages of 4 cestodes), and 14 species of arthropod parasites. The helminths harboured in common by the 2 groups of warthogs are *O. mwanzae, P. sexalatus, P. vivipara* and *Moniezia/Paramoniezia* sp. and the arthropods are *E. larina, H. phacochoeri, Hyalomma truncatum, R. simus* and *O. porcinus porcinus*.

Helminths

Ascaris phacochoeri

This helminth has previously been recovered from warthogs in Zululand by Ortlepp (1939). The percentage of warthogs infested (30,8 %) in the present survey is identical to that of a group of domestic pigs infested with *Ascaris suum* (Horak, 1978a). These pigs had been consigned by farmers to the Pretoria Municipal Abattoir over a period of 1 year. The mean burden of adult *A. phacochoeri* (0,67 worms, range 0–7 worms) in the warthogs is, however, slightly lower than that of adult *A. suum* in the domestic pigs (2 worms, range 0–15 worms).

Impalaia tuberculata

This nematode, and the related species *Impalaia nudicollis,* are usually recovered from antelope, particularly impala *(Aepyceros melampus)* (Horak, 1978d) and blesbok *(Damaliscus dorcas phillipsi)* (Horak, 1978c). However, *I. nudicollis* has been recovered from warthogs in Namibia (Horak, Biggs, Hanssen & Hanssen, 1983), while those examined in the Kruger National Park harboured *I. tuberculata*. The measurements of both these worms from the warthogs were considerably smaller than those given by Gibbons, Durette-Desset & Daynes (1977) and Boomker (1977) in their reviews of the genus *Impalaia*. Contrary to the findings for *I. nudicollis* in the Namibian warthogs, in which few worms were adult, the majority of *I. tuberculata* in the Kruger National Park warthogs were adult (Table 1). Nevertheless the small size of the latter worms indicates that warthogs are not definitive hosts of this nematode.

Mushidia *spp.*

Ortlepp (1964) noted that there were no worms of the genus *Murshidia* in warthogs from Moçambique, while warthogs at Pilgrim's Rest and in Zululand were infested. Moçambique lies to the east and north of the Kruger National Park, Pilgrim's Rest to the west and Zululand to the south-east. It is possible that the warthogs from Moçambique examined by Ortlepp (1964), were by chance not infested with *Murshidia* spp. If, however, *Mushidia* spp. are indeed absent in warthogs in Moçambique it would be interesting to determine the exact boundary of infestation between the Kruger National Park and that territory. Very large burdens of worms of this genus are possible as 1 of the warthogs from Crocodile Bridge harboured a total of 48 000 immature and adult *M. hamata* and *M. pugnicaudata* and 1 from Pafuri harboured 40 775 immature and adult *M. hamata*.

Oesophagostomum *spp.*

Ortlepp (1964) identified *O. mocambiquei, O. mwanzae* and *O. santos-diasi* in material collected from warthogs in Moçambique and Pilgrims' Rest. No oesophagostomes were present in the specimens he examined from warthogs in Zululand. *O. mwanzae* has a very widespread distribution being present in warthogs in northern Moçambique and at Pilgrim's Rest (Ortlepp, 1964), in the Kruger National Park (present survey) and in northern Namibia (Horak, Biggs, Hanssen & Hanssen, 1983). In both Namibia and the Kruger National Park it was not the dominant oesophagostome, being outnumbered by *Oesophagostomum mpwapwae* at the former and *O. mocambiquei* at the latter locality.

The largest total number of immature and adult *Oesophagostomum* spp. recovered from a single warthog in the present survey was 7 400 worms, compared with 30 510 adult worms from a warthog in Namibia (Horak, Biggs, Hanssen & Hanssen, 1983).

Physocephalus sexalatus

Horak, Biggs, Hanssen & Hanssen (1983) recovered speak burdens of this nematode from January to March in warthogs from northern Namibia, while Horak (1978b) found that the related *Ascarops strongylina* was most abundant in domestic pigs in the Transvaal from November to March. No pattern of seasonal abundance could be determined in the present survey. Ortlepp (1964) has recorded both *A. strongylina* and *P. sexalatus* from bushpigs *(Potamochoerus porcus)* in the northern Transvaal, but *A. strongylina* has apparently not been recovered from warthogs (Round, 1968).

Probstmayria vivipara

As in the case of the animals in Namibia (Horak, Biggs, Hanssen & Hanssen, 1983) extremely large burdens, of which we did not attempt to ascertain the numbers, were present.

Strongyloides *sp.*

The fact that a 1-month-old animal and another young animal were infested with this worm seems to indicate a milk-borne route of infestation as in the case of *Strongyloides papillosus* in sheep and goats (Moncol & Grice, 1974).

Trichostrongylus *spp.*

We think that the small number of warthogs infested with *Trichostrongylus falculatus* and *T. instabialis,* and the small burdens of these worms in the infested warthogs, indicate that these are accidental infestations, as the true hosts are 1 or more of the antelope species in the park.

In the same way that *Trichostrongylus axei* appears to be an abomasal parasite in both domestic ruminants and horses (Soulsby, 1968), *T. thomasi* fills this niche in antelope (Round, 1968; Horak, Meltzer & De Vos, 1982; Horak, Brown, Boomker, De Vos & Van Zyl, 1982; Horak, De Vos & Brown, 1983; Boomker, Horak & De Vos, 1986), Burchell's zebras (Scialdo, Reinecke & De Vos, 1982) and warthogs (present survey).

Larval cestodes

The *Echinococcus* sp. cysts could have originated from adult cestodes of this genus present in a variety of carnivore species in the park. Adult *Taenia crocutae* and *Taenia hyaenae* are parasites of hyaenas while adult *Taenia regis* is found in lions (Round, 1968).

Arthropods

Echidnophaga *spp.*

Both *E. inexpectata* and *E. larina* are stick-tight fleas found firmly attached mainly along the softer undersides of the warthogs. *E. larina* is frequently encountered on warthogs, while *E. inexpectata* is supposedly a rarer parasite of these animals (Haeselbarth, Segerman & Zumpt, 1966). Although because of their stick-tight habit, it was not possible to obtain exact counts for either species in the present survey, the numbers of *E. inexpectata* generally seemed to exceed those of *E. larina.*

Whether the peak early winter and spring abundances of these fleas were real or due to large variations in individual burdens could not be ascertained. In Namibia no clear pattern of seasonal abundance of *E. larina* on warthogs could be determined (Horak, Biggs, Hanssen & Hanssen, 1983).

Moeopsylla sjoestedti

This is a jumping flea and was found mainly around the necks and heads of the warthogs. This species has been recovered from warthogs in east Africa from Kenya in the north to the eastern Transvaal Lowveld in the south (Haeselbarth *et al.*, 1966).

Haematopinus phacochoeri

This is the large sucking louse of warthogs (Ledger, 1980). In Namibia peak burdens were present on the warthogs in September of 1 year and during June of the following year (Horak, Biggs, Hanssen & Hanssen, 1983). In the present survey there was a clear peak of abundance of both nymphae and adults from July to September.

The months of peak abundance are also the months during which the available feed is at its driest. Perhaps the warthogs conserve energy during this time of nutritional stress by reducing the time spent on grooming and increasing the time devoted to foraging, hence the increasae in lice burdens.

Amblyomma hebraeum

Excluding the burdens of the 1 warthog carrying exceptionally large numbers of adult ticks (Table 2), warthogs must still be considered 1 of the preferred hosts of the adults of this tick. They carry more adult ticks than do blue wildebeest (Horak, De Vos & Brown, 1983), Burchell's zebras (Horak *et al.*, 1984), large and small carnivores (Horak, Jacot Guillarmmod, Moolman & De Vos, 1987) and impala (Horak, Boomker & De Vos, unpublished data, 1987) examined in the park. The ratio of larvae to nymphae to adults indicates a high proportion of adults, and this suggests that the warthog is a better host of adult *A. hebraeum* than of the immature stages.

The very large burdens of *A. hebraeum* recovered from the warthogs shot during the drought of 1982 do not imply that these ticks prefer dry conditions. They reflect rather that the animals' resistance was markedly reduced because of nutritional stress, and that they probably conserved energy by reducing grooming to a minimum, both these factors presumably leading to increased tick burdens (O'Kelly & Seifert, 1969).

The seasonal abundance of immature *A. hebraeum* on the warthogs is similar to that observed by Knight & Rechav (1978) on kudu, by Rechav (1982) on cattle, and by MacIvor & Horak (1984) on goats in the eastern Cape Province. The period of adult abundance on the warthogs, however, was longer than that observed on the other hosts.

Rhipicephalus appendiculatus/zambeziensis

Judging by the numbers recovered, warthogs are not important hosts of these ticks and particularly not of the adults. Burchell's zebra (Horak *et al.*, 1984) and more particularly impala and kudu (Horak, Boomker & De Vos, unpublished data, 1987) are better hosts. The seasonal abundance of all stages of development is similar to that of *R. appendiculatus* on impala and cattle in the northern Transvaal (Horak, 1982). The larvae of the 2 species were most abundant on the warthogs during the same months in which maximum abundance of this developmental stage has been recorded on blue wildebeest in the park (Horak, De Vos & Brown, 1983). The nymphal peak of *R. appendiculatus* on the warthogs corresponds to that on blue wildebeest and Burchell's zebra in the park (Horak, De Vos & Brown, 1983; Horak *et al.*, 1984).

Not only are *R. appendiculatus* and *R. zambeziensis* similar in appearance (Walker, Norval & Corwin, 1981), but their distributions overlap in certain regions and their seasonal abundance is similar (Norval, Walker & Colborne, 1982; present study).

Rhipicephalus kochi

This tick has previously been recovered from animals at Pafuri (Gertrud Theiler, unpublished data, 1964, as *Rhipicephalus neavei;* Horak, Potgieter, Walker, De Vos & Boomker, 1983). This is as yet the only site in the Republic of South Africa at which *R. kochi* is known to occur (Clifford, Walker & Keirans, 1983). The warthog does not appear to be a preferred host of this tick as no immature stages and few adults were recovered. Kudu, nyala and bushbuck examined at Pafuri during October 1981 harboured fairly large numbers of nymphae and adults (Horak, Potgieter, Walker, De Vos & Boomker, 1983), while only 1 of the 2 warthogs examined at the same time was infested and that with only 4 male *R. kochi.*

Rhipicephalus simus

In the park the adults of this tick seem to prefer monogastric animals such as Burchell's zebra (Horak *et al.*, 1984), carnivores (Horak *et al.*, 1987) and warthogs (present survey) rather than ruminants. Norval & Mason (1981) state that the larger ungulate and carnivore species are the most important wild hosts with warthogs frequently being parasitized.

The seasonal abundance on the warthogs roughly corresponds to the times of maximum abundance on Burchell's zebra in the park (Horak *et al.*, 1984) and on cattle in the northern Transvaal (Horak, 1982).

Other ixodid ticks

We consider *Boophilus decoloratus, H. truncatum* and *Rhipicephalus evertsi evertsi* to be accidental infestations on the warthogs. They are more a reflection of ticks present in the environment rather than host preference.

Ornithodoros porcinus porcinus

Chorley (1943) cited by Hoogstraal (1956) and Horak, Biggs, Hanssen & Hanssen (1983) recovered this tick on warthogs, although it is usually encountered in their burrows (Hoogstraal, 1956). In the present study 1 animal harboured 97 nymphae and another 107. These ticks had probably not completed feeding when the warthogs left their burrows in the mornings and some would presumably have remained on the animals until they returned to the burrows in the evenings. This would probably explain how the ticks spread from 1 burrow to the next.

Linguatula nuttalli

The recovery of the nymphae of this pentastomid from a high proportion of warthogs is a reflection of the large number of lions, the final host of this parasite, in the park. Horak, De Vos & Brown (1983) have recovered the nymphae of *L. nuttalli* from a fairly large proportion of blue wildebeest in the park.

Blood parasites

Trypanosomes, resembling *Trypanosoma vivax*, were seen by Curson (1928) in the blood of a single warthog in Zululand. Neitz (1931) examined blood, spleen and lymphnode smears of 56 warthogs from Zululand and, with the exception of 5 animals with microfilarial infections, no other haemoparasites were observed. In a subsequent investigation, 7 out of 34 warthogs in Zululand were found to be infected with microfilariae and a small *Theileria*-like piroplasm was found in the blood of 1 of these animals (Neitz, 1933). According to Neitz (1933) this was the 1st observation of small piros in the red cells of a warthog. No trypanosomes were seen.

In the persent survey an effort was made to detect *Theileria*-like parasites in the blood smears of the warthogs, but none were found. More animals from different geographical regions should be examined, however, as vector distribution may play a role in the prevalence of this parasite.

ACKNOWLEDGEMENTS

We wish to express our thanks to the National Parks Board of Trustees who made the warthogs available to us. We gratefully acknowledge the technical assistance of Mrs Moira R. Brown and Mr B. D. de Klerk. Dr E. M. Nevill of the Veterinary Research Institute, Onderstepoort, pointed out the differences between *E. larina* and *E. inexpectata*, and Dr Jane B. Walker, of the same institute, identified *R. kochi*. Prof. Anna Verster, of the Faculty of Veterinary Science, University of Pretoria, identified the larval stages of the cestodes.

This research was funded by the University of Pretoria and the Council for Scientific and Industrial Research.

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Printed by the Government Printer, Private Bag X85, Pretoria, 0001

Onderstepoort Journal of Veterinary Research, 65:137–141 (1998)

RESEARCH COMMUNICATION

Helminths and bot fly larvae of wild ungulates on a game ranch in Central Province, Zambia

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ABSTRACT

ZIEGER, U., BOOMKER, J., CAULDWELL, A.E. & HORAK, I.G. 1998. Helminths and bot fly larvae of wild ungulates on a game ranch in Central Province, Zambia. *Onderstepoort Journal of Veterinary Research*, 65:137–141

Helminths and bot fly larvae were collected from 11 wild ungulate species on a game ranch in the Central Province of Zambia. New host-parasite records are: *Calicophoron* sp. from defassa waterbuck *Kobus ellipsiprymnus defassa* and Kafue lechwe *Kobus leche kafuensis*; *Avitellina centripunctata*, *Gaigeria pachyscelis* and *Gedoelstia cristata* from tsessebe *Damaliscus lunatus lunatus*; *Cooperia rotundispiculum* from common reedbuck *Redunca arundinum*; *Dictyocaulus filaria* from greater kudu *Tragelaphus strepsiceros*; *Dictyocaulus* sp. from tsessebe and defassa waterbuck and *Strobiloestrus* sp. from sable antelope *Hippotragus niger*. Most of the other parasites collected are first records for Zambia and thus extend the distribution ranges of several species.

Keywords: Bot fly larvae, helminths, ungulates, Zambia

INTRODUCTION

Since the first private ranches were licensed in 1989 game ranching is a growing industry in Zambia. The opportunity arose to collect parasites on one of these ranches during meat inspection of wild animals that had been shot either for venison, for trophies or because of injuries. The purpose of this investigation was to document new host-parasite records and to extend records of the distribution ranges of parasites of African ungulates. The animals' parasite burdens were not counted, but merely estimated subjectively.

MATERIALS AND METHODS

The animals were all examined on Mtendere Game Ranch (15°05´S, 28°15´E) situated approximately 20 km north of Lusaka in the Chisamba District of Central Province, Zambia. The ranch covers an area of 960 ha and lies within the miombo woodland zone of Zambia. At the time of the investigation it accommodated 18 larger wildlife species at a stocking density of one large stock unit per 4,7 ha.

Thirty-eight animals were examined between December 1995 and November 1996, comprising one Burchell's zebra *Equus burchellii*, 12 impala *Aepyceros melampus*, three tsessebe *Damaliscus lunatus lunatus*, one Lichtenstein's hartebeest *Sigmoceros lichtensteinii*, two eland *Taurotragus oryx*, three bushbuck *Tragelaphus scriptus*, four greater kudu *Tragelaphus strepsiceros*, two sable antelope *Hippotragus niger*, six defassa waterbuck *Kobus ellipsiprymnus defassa*, two Kafue lechwe *Kobus leche kafuensis*, one puku *Kobus vardonii* and one common reedbuck *Redunca arundinum*. Immediately after death their carcasses were transported to a nearby abattoir. The thorax and abdominal cavity were opened, examined for helminths and eviscerated. The gastro-intestinal tract was opened in its entirety, and its contents, together with the thoracic organs, liver, kidneys, paranasal sinuses and skins were examined for parasites

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Accepted for publication 2 April 1998—Editor

according to standard necropsy procedures. Macroscopically visible parasites or samples of these parasites were collected and stored in 70% ethyl alcohol for later identification.

RESULTS AND DISCUSSION

The trematode and cestode species recovered are listed in Table 1, the nematodes in Table 2 and the bot fly larvae in Table 3. The tables include references to the first record of each parasite per host species in their natural environment, as well a comment as to whether this is a first record for Zambia.

Eight new host-helminth associations were recorded in this study. As only a few studies on the helminths of wildlife have ever been undertaken in Zambia, most of the findings are new for this country. Two of the bot fly larvae recovered are also new host-parasite records.

The wild ruminants generally appeared to harbour small burdens and in most cases only a few parasites were encountered in each individual. However, *Calicophoron* sp. as well as *Stilesia hepatica* was found in large numbers in the defassa waterbuck. The single Burchell's zebra examined seemed to be heavily infected with *Gastrodiscus aegyptiacus*, *Anoplocephala perfoliata* and *Strongylus vulgaris*.

It would appear as if several of the helminth species collected in this study were not particulariy host specific, as they were often found in more than one host species. The high stocking density of wildlife on the ranch would facilitate such cross-infection (Horak

TABLE 1 Trematodes and cestodes recovered from wild ungulates on a game ranch in Central Province, Zambia

Host and helminth species	Number of animals infected	First record	New record for Zambia
Burchell's zebra (1 animal)			
Gastrodiscus aegyptiacus	1	Le Roux 1932	No
Anoplocephala perfoliata	1	v. Linstow 1901	Yes
Impala (12 animals)			
Calicophoron sp.	1	Ortlepp 1961[a]	Yes
Stilesia hepatica	0	Meeser 1952	Yes
Cysticercus sp.	1	Meeser 1952	No
Moniezia benedeni	2	Hudson 1934	Yes
Tsessebe (3 animals)			
Calicophoron sp.	1	Eduardo 1982a, b	Yes
Avitellina centripunctata	1	This paper	Yes
Eland (2 animals)			
Moniezia benedeni	1	Hudson 1934	Yes
Bushbuck (3 animals)			
Stilesia hepatica	1	Fuhrman 1909	Yes
Greater kudu (4 animals)			
Fasciola gigantica	1	Condy 1972	No
Sable antelope (2 animals)			
Calicophoron sp.	1	Ortlepp 1961[a]	Yes
Defassa waterbuck (6 animals)			
Calicophoron sp.	6	This paper	Yes
Fasciola gigantica	1	Stunkard 1929	Yes
Stilesia hepatica	6	Baer & Fain 1955	Yes
Kafue lechwe (2 animals)			
Calicophoron sp.	1	This paper	Yes
Fasciola gigantica	1	Gallagher *et al.* 1972	No
Schistosoma sp.	1	Le Roux 1932	No

[a] *C. calicophorum*

1980). The presence of *Haemonchus contortus* on the ranch warrants attention as it is established in five host species. It is a bloodsucking parasite that can be pathogenic even at low levels of infection. *Haemonchus* sp. infection was suspected as the main cause of mortality in sable antelope in Zimbabwe under particularly moist conditions (Grobler 1981). Another potentially lethal parasite is *Fasciola gigantica*, which has been incriminated in mortalities in several wildlife species (Hammond 1972; Condy 1972; Knottenbelt 1990). However, in the present study only three animals were infected. Despite repeated intensive searches involving all water sources on the ranch for the fresh water snail *Lymnaea natalensis*, the principle intermediate host of this fluke in southern Africa, only two empty shells were found

TABLE 2 Nematodes recovered from wild ungulates on a game ranch in Central Province, Zambia

Host and nematode species	Number of animals infected	First record	New record for Zambia
Burchell's zebra (1 animal)			
Cylicocyclus insigne	1	Le Roux 1932	No
Draschia sp.	1	Mönnig 1928[a]	No
Strongylus vulgaris	1	Leiper 1909	Yes
Impala (12 animals)			
Cooperioides hamiltoni	1	Mönnig 1932b	Yes
Cooperioides hepaticae	4	Ortlepp 1938	Yes
Cooperioides sp.	3	Mönnig 1932b[b]	Yes
Gaigeria pachyscelis	1	Meeser 1952	Yes
Haemonchus contortus	1	Meeser 1952	Yes
Tsessebe (3 animals)			
Agriostomum cursoni	1	Mönnig 1932a	Yes
Dictyocaulus sp. females	2	This paper	Yes
Gaigeria pachyscelis	1	This paper	Yes
Impalaia sp. females	1	Boomker 1977[c] Gibbons *et al* 1977	Yes
Lichtenstein's hartebeest (1 animal)			
Haemonchus contortus	1	Le Roux 1934	No
Eland (2 animals)			
Cooperia rotundispiculum	1	Boomker 1991	Yes
Haemonchus contortus	1	Mönnig 1933	Yes
Oesophagostomum sp.	1	Mönnig 1932b[d]	Yes
Greater kudu (4 animals)			
Agriostomum gorgonis	1	Le Roux 1934	No
Cooperia rotundispiculum	1	Boomker *et al.* 1991	Yes
Dictyocaulus filaria	1	This paper	Yes
Elaeophora sagitta	3	Mönnig 1926	Yes
Haemonchus contortus	1	Veglia 1919	Yes
Defassa waterbuck (6 animals)			
Dictyocaulus sp. females	1	This paper	Yes
Kafue lechwe (2 animals)			
Haemonchus contortus	1	Le Roux 1930	Yes
Reedbuck (1 animal)			
Cooperia rotundispiculum	1	This paper	Yes
Setaria bicoronata	1	Yeh 1959	Yes

[a] *D. megastoma*
[b] *C. hamiltoni*
[c] *I. tuberculata*
[d] *O. walkeri*

TABLE 3 Bot fly larvae recovered from wild ungulates on a game ranch in Central Province, Zambia

Host and bot fly species	Number of animals infected	First record	New record for Zambia
Burchell's zebra (1 animal)			
Gasterophilus haemorrhoidalis	1	Zumpt 1965	No
Gasterophilus meridionalis	1	Zumpt 1965	No
Gasterophilus nasalis	1	Zumpt 1965	No
Gasterophilus pecorum	1	Zumpt 1965	Yes
Gasterophilus ternicinctus	1	Zumpt 1965	No
Tsessebe (3 animals)			
Gedoelstia cristata	1	This paper	Yes
Oestrus variolosus	1	Zumpt 1965	No
Sable antelope (2 animals)			
Strobiloestrus sp.	1	This paper	Yes
Kafue lechwe (2 animals)			
Strobiloestrus sp.	1	Zumpt 1961[a]	No

[a] *S. vanzyli*

(Zieger 1998). It is possible that some *F. gigantica* were introduced onto the ranch with their mammal hosts during the initial game stocking programme in 1990/1991. If indeed there are no intermediate snail hosts on the ranch, the infection could be self-limiting.

ACKNOWLEDGEMENTS

We thank Mr and Mrs M. O'Donnell who provided U. Zieger and A.E. Cauldwell with accommodation and permitted us to undertake this study on their ranch. We are grateful to Mr C. Harvey, whose abattoir facilities were used.

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PARASITES OF SOUTH AFRICAN WILDLIFE. VIII. HELMINTH AND ARTHROPOD PARASITES OF WARTHOGS, *PHACOCHOERUS AETHIOPICUS*, IN THE EASTERN TRANSVAAL

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ABSTRACT

BOOMKER, J., HORAK, I. G., BOOYSE, D. G. & MEYER, SANTA, 1991. Parasites of South African wildlife. VIII. Helminth and arthropod parasites of warthogs, *Phacochoerus aethiopicus*, in the eastern Transvaal. *Onderstepoort Journal of Veterinary Research*, 58, 195–202 (1991)

Helminth and arthropod parasites were collected from 41 warthogs, *Phacochoerus aethiopicus*, in the Hoedspruit Nature Reserve, eastern Transvaal. This reserve consists of a military base, which is a restricted area and is surrounded by a reserve, which is open to the public. Eleven nematode species, 1 or 2 cestode species and the larvae of 2 cestode species were recovered from the animals in the reserve, and 8 nematode species and 1 or 2 cestode species were recovered from those in the military base.

Oesophagostomum spp. were generally most abundant in warthogs in the reserve during the cooler months of the year, while *Probstmayria vivipara* also occurred in peak numbers during the cooler months, with an additional peak in October and November 1988 in warthogs in the reserve and the base, respectively. No pattern of seasonal abundance could be determined for the other helminth species.

The warthogs also harboured 8 ixodid and 1 argasid tick species, 3 flea species and 1 louse species. Adult and immature *Haematopinus phacochoeri* were most numerous during August and September, and the largest numbers of adult *Rhipicephalus simus* were present from December to April.

INTRODUCTION

The seasonal abundance of endo- and ectoparasites of warthogs, *Phacochoerus aethiopicus*, in northern Namibia and in the Kruger National Park (KNP) in the eastern Transvaal have recently been reported (Horak, Biggs, Hanssen & Hanssen, 1983; Horak, Boomker, De Vos & Potgieter, 1988). The warthogs from Namibia were infested with 9 nematode species, 1 or 2 cestode species, 6 ixodid tick species, 1 argasid tick species, a flea and a louse species and the larvae of a calliphorid fly. Those from the KNP harboured 13 nematode species, 1 trematode species, 1 or 2 cestode species, the larval stages of 4 cestode species, 7 ixodid tick species, 1 species of argasid, 3 flea species, 1 louse species and the nymphs of a pentastomid.

This paper describes a similar survey conducted on warthogs in the Hoedspruit Nature Reserve which is also situated in the eastern Transvaal Lowveld.

MATERIALS AND METHODS

Survey area

The warthogs were all shot in the Hoedspruit Nature Reserve (HNR) which is situated in a vegetation zone classified as Lowveld (Acocks, 1988). The temperature is warm to hot in summer and mild in winter, and frost does not occur.

The HNR is owned by the South African Defence Force and comprises approximately 4 000 ha. It consists of an inner area of about 2 000 ha, the restricted military base, around which lies another 2 000 ha, the reserve, which is open to the public. The base is separated from the reserve by a series of security fences, thus making it impossible for warthogs on either side to pass through. The outer fence of the reserve, however, is of such a nature that warthogs from the surrounding privately owned game farms can pass through with ease.

Climatological data

The mean monthly maximum and minimum atmospheric tempatures as well as the total monthly rainfall were recorded during the survey period.

Survey animals

With the exception of March 1989, when none could be located, warthogs were shot each month for 12 consecutive months from August 1988 to July 1989. Although often unsuccessful, an attempt was made at each occasion to collect the same number of warthogs of the same ages and sexes from the reserve and the base. A total of 41 warthogs was shot, of which 5 adult males, 11 adult females, 5 subadult males, 2 subadult females 1 juvenile male and 4 juvenile females were shot in the reserve and 1 adult male, 4 adult females, 2 subadult males, 2 subadult females, 1 juvenile male and 3 juvenile females were shot on the base.

Parasite recovery

The carcasses were transported to a field laboratory where they were eviscerated and macroscopically visible parasites removed and preserved in 70 % alcohol.

The carcasses were skinned and eviscerated, and the gastro-intestinal tracts were divided into the stomachs, the small intestines and the large intestines, and placed in shallow, flat-bottomed plastic trays. The stomachs were cut open and the ingesta carefully removed so as not to disturb the underlying mucosa. The ingesta were discarded, but the stomach was thoroughly washed in normal saline and the volume of the resulting suspension measured. The small and the large intestines were opened separately with bowel scissors and washed in saline. The washings were added to the respective ingesta. The volumes of the ingesta were measured and poured into separate plastic buckets. A $\frac{1}{4}$th aliquot by volume was made of the ingesta of each of the small intestines and a $\frac{1}{5}$th aliquot of the ingesta of each of the large intestines. The worms in the various aliquots as well as those in the various stomach contents were killed by adding an equal volume of boiling saline to each. The suspensions were then individually washed over a sieve with apertures of 0,15 mm and the residues preserved in separate bottles in 10 % formalin. Digests of the gastro-intestinal mucosae were not done.

The hearts, lungs and livers of the first 16 animals were processed for helminth recovery as described by Boomker, Horak & De Vos (1989) and examined. When no parasites were found, these organs were no longer processed or examined.

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Received 23 May 1991—Editor

TABLE 1 Amended list of the helminth parasites of warthogs in the Republics of South Africa and Namibia with reference to the first record and the authors of the descriptions used to assist with the identification

Helminth species	First record	Identification
Trematodes		
Gastrodiscus aegyptiacus Railliet, 1893	Horak *et al.*, 1988	+
Schistosoma sp.	Horak *et al.*, 1988	+
Cestodes		
Echinococcus sp. larvae	Horak *et al.*, 1988	+
Moniezia mettami Baylis, 1934	Ortlepp, 1964	Baylis, 1934
Paramoniezia phacochoeri Baylis, 1927	Baylis, 1927	Baylis, 1927
Taenia crocutae larvae	Horak *et al.*, 1988	+
Taenia hyaenae larvae	Horak *et al.*, 1988	+
Taenia regis larvae	Horak *et al.*, 1988	+
Nematodes		
Ascaris phacochoeri Gedoelst, 1916	Ortlepp, 1939	Ortlepp, 1939
Cooperia hungi Mönnig, 1931	This paper	Gibbons, 1981
Haemonchus krugeri Ortlepp, 1964	Horak *et al.*, 1988	+
Impalaia nudicollis Mönnig, 1931	Horak *et al.*, 1983	+
Impalaia tuberculata Mönnig, 1923	Horak *et al.*, 1988	Boomker, 1977
Microfilaria sp. (*sensu* Neitz, 1931)	Neitz, 1931	+
Microfilariae	Palmieri *et al.*, 1985	+
Murshidia hamata Daubney, 1923	Daubney, 1923	Daubney, 1923
Murshidia pugnicaudata (Leiper, 1909)	Daubney, 1923	Daubney, 1923
Odontogeton phacochoeri Allgrén 1921	Allgrén, 1921*	+
Oesophagostomum mocambiquei Ortlepp, 1964	Ortlepp, 1964	Ortlepp, 1964
Oesophagostomum mpwapwae Duthy, 1947	Horak *et al.*, 1983	+
Oesophagostomum mwanzae Daubney, 1924	Ortlepp, 1964	Ortlepp, 1964
Oesophagostomum roubaudi Daubney, 1926	Horak *et al.*, 1983	+
Oesophagostomum santosdiasi Ortlepp, 1964	Ortlepp, 1964	+
Oesophagostomum simpsoni Goodey, 1924	Ortlepp, 1964	+
Physocephalus sexalatus Diesing, 1861	Horak *et al.*, 1983	Yorke & Maplestone, 1926
Probstmayria vivipara Ransom, 1911	Le Roux, 1940	Yorke & Maplestone, 1926
Strongyloides spp.	Horak *et al.*, 1988	+
Trichostrongylus falculatus Ransom, 1911	Horak *et al.*, 1988	+
Trichostrongylus deflexus Boomker & Reinecke, 1989	Horak *et al.*, 1983	Boomker & Reinecke, 1989
Trichostrongylus thomasi Mönnig, 1932	Horak *et al.*, 1988	Mönnig, 1932
Trichuris sp.	Horak *et al.*, 1988	+

\+ Not found in this survey

* After Round (1968)

The ectoparasites were collected as described by Horak *et al.* (1988).

Parasite counts and identification

The lung, heart and liver washings of the first 16 animals, as well as the washings of the stomach walls and the aliquots of the small intestinal ingesta were examined under a stereoscopic microscope and all the worms removed.

The ingesta of the large intestines were examined in a flat-bottomed tray and all the macroscopically visible worms removed. Because of the large numbers of *Probstmayria vivipara* present, a 1/100th aliquot was made of each of the large intestinal ingesta after they had been macroscopically examined. The aliquot was examined under a stereoscopic microscope and *Probstmayria vivipara* counted.

With the exception of *Probstmayria vivipara,* all the worms were cleared in lactophenol and examined under a standard microscope with Nomarski's differential intereference illumination. They were identified with the aid of the descriptions by the authors listed in Table 1. This table also lists the helminth recovered to date from warthogs in South Africa and Namibia.

The ectoparasites were counted as described by Horak *et al.* (1988).

RESULTS

The total monthly rainfall and the mean monthly minimum and maximum atmospheric temperatures for the period August 1988–July 1989 are graphically illustrated in Fig. 1.

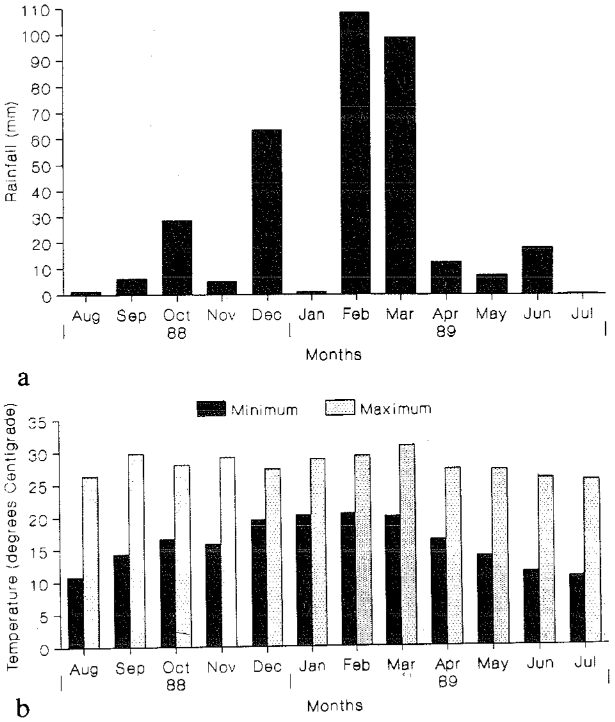

FIG. 1 Mean monthly rainfall (a) and minimum and maximum temperatures (b) at the Hoedspruit Nature Reserve

Helminths

The total numbers of helminths recovered from all the warthogs are summarised in Table 2.

TABLE 2 The helminths recovered from 41 warthogs from the Hoedspruit Nature Reserve

Helminth species	Larvae	Adults	Total	Number of warthogs infected
Reserve (28 warthogs)				
*Moniezia/Paramoniezia**	#	109	109	12
Taenia regis	2	#	2	2
Echinococcus	1	#	1	1
Ascaris phacochoeri	0	114	114	13
Cooperia hungi	0	100	100	1
Impalaia tuberculata	0	150	150	5
Murshidia hamata	+	34 361	34 361	28
Murshidia pugnicaudata	+	6 215	6 215	28
Murshidia spp.	118	—	118	8
Oesophagostomum mocambiquei	+	90 058	90 058	27
Oesophagostomum mwanzae	+	37 684	37 684	28
Oesophagostomum spp.	2 901	—	2 901	13
Physocephalus sexalatus	80	9 494	9 574	23
Probstmayria vivipara	$	$	267,255 million	28
Trichostrongylus deflexus	0	20	20	2
Trichostrongylus thomasi	0	60	60	4
Trichostrongylus spp. females	—	50	50	5
Mean nematode burden**	111	6 368	6 479	
Base (13 warthogs)				
*Moniezia/Paramoniezia**	#	53	53	5
Ascaris phacochoeri	0	32	32	5
Murshidia hamata	+	21 734	21 734	13
Murshidia pugnicaudata	+	4 588	4 588	12
Murshidia spp.	222	—	222	5
Oesophagostomum mocambiquei	+	8 507	8 507	12
Oesophagostomum mwanzae	+	4 090	4 090	12
Oesophagostomum spp.	94	—	94	3
Physocephalus sexalatus	0	610	610	10
Probstmayria vivipara	$	$	148,331 million	13
Trichostrongylus spp. females	—	10	10	1
Mean nematode burden**	24	3 044	3 068	

* Scoleces
** Excluding *Probstmayria vivipara*
\# Not found in warthogs
$ Larvae and adults not counted separately
\+ Counted together under the respective genera
— Not applicable

Eleven namatode species, 1 or 2 cestode species and the larval stages of 2 cestode were recovered from warthogs shot in the reserve. Of these, *Murshidia hamata, Murshidia pugnicaudata, Oesophagostomum mwanzae,* and *Probstmayria vivipara* occurred in all the warthogs. *Oesophagostomum mocambiquei* was recovered from 27 warthogs and *Physocephalus sexalatus* from 23. The remaining nematodes occured in less than 50 % of the animals examined.

Probstmayria vivipara was the most abundant of the nematodes, followed by *Oesophagostomum mocambiquei, Oesophagostomum mwanzae, Murshidia hamata, Physocephalus sexalatus* and *Murshidia pugnicaudata.*

Individual adult nematode burdens, excluding *Probstmayria vivipara* varied from 445 to 41 950 and the mean total adult nematode burden, excluding *Probstmayria vivipara,* was 6 368.

Eight species of nematodes and 1 or 2 cestode species were recovered from the 13 warthogs shot in the base. *Probstmayria vivipara* and *Murshidia hamata* were recovered from all these warthogs and *Murshidia pugnicaudata, Oesophagostomum mocambiquei* and *Oesophagostomum mwanzae* from 12 warthogs each. *Physocephalus sexalatus* occurred in 10 animals.

Probstmayria vivipara was again the most abundant nematode, followed by *Murshidia hamata, Oesophagostomum mocambiquei, Murshidia pugnicaudata* and *Oesophagostomum mwanzae.*

The individual adult nematode burdens, excluding *Probstmayria vivipara,* varied from 91 to 7 260 and the mean total adult nematode burden, excluding *Probstmayria vivipara,* was 3 044.

Ascaris phacochoeri and the *Moniezia/Paramoniezia* spp. were only recovered from animals younger than 18 months, while *Oesophagostomum* spp., *Murshidia* spp., *Physocephalus sexalatus* and *Probstmayria vivipara* were already present in the youngest animal in the survey, a male, 3–4 months old, shot in the reserve during August 1988.

No differences in the mean monthly nematode burdens or nematode species composition between the ages or the sexes of the warthogs shot at either locality, were evident.

The seasonal fluctuations of *Oesophagostomum* spp., *Murshidia* spp. and *Probstmayria vivipara* are graphically illustrated in Fig. 2–4.

In both groups of warthogs, peaks in the numbers of *Oesophagostomum* spp. occurred during the cooler months of the year. The high peak seen in warthogs from the reserve shot during August 1988, however, is due to 1 animal harbouring 30 700 *O. mocambiquei,* and probably does not reflect the true situation. No seasonal pattern of abundance was evident for the *Murshidia* spp. The largest numbers of *Probstmayria vivipara* were recovered during the cooler months of the year, with a peak occurring during October and November 1988 in the warthogs from the reserve and the base, respectively.

TABLE 3 Arthropod parasites recovered from 28 warthogs from the Hoedspruit Nature Reserve, eastern Transvaal

Arthropod species	Total numbers of arthropods recovered					Number of warthogs infested
Fleas	Males		Females		Total	
Echidnophaga inexpectata/larina	7 098*				7 098	27
Moeopsylla sjoestedti	72		132		204	18
Lice	Nymphs	Males	Females		Total	
Haematopinus phacochoeri	1 228	170	200		1 598	14
Ixodid ticks	Larvae	Nymphs	Males	Females	Total	
Amblyomma hebraeum	158	1 228	254	80 (0)	1 720	28
Amblyomma marmoreum	2	0	0	0	2	1
Boophilus decoloratus	126	0	0	0	126	3
Hyalomma truncatum	0	0	10	4 (0)	14	3
Rhipicephalus appendiculatus	2	0	0	0	2	1
Rhipicephalus evertsi evertsi	2	2	0	0	4	2
Rhipicephalus simus	0	0	82	40 (2)	122	16
Rhipicephalus zambeziensis	0	4	2	0	6	2
Argasid ticks	Larvae	Nymphs	Adults		Total	
Ornithodoros porcinus porcinus	0	232	0		232	13

() = Number of maturing female ticks, i.e. the idiosoma of *A. hebraeum* > 9,0 mm; *H. truncatum* > 7,5 mm; *R. simus* > 6,0 mm
* = Sexes not determined

TABLE 4 Arthropod parasites recovered from 13 warthogs on a military base near Hoedspruit, eastern Transvaal

Arthropod species	Total numbers of arthropods recovered					Number of warthogs infested
Fleas	Males		Females		Total	
Echidnophaga inexpectata/larina	1 036*				1 036	13
Moeopsylla sjoestedti	2		6		8	3
Lice	Nymphs	Males	Females		Total	
Haematopinus phacochoeri	534	46	68		648	8
Ixodid ticks	Larvae	Nymphs	Males	Females	Total	
Amblyomma hebraeum	0	18	2	2 (2)	30	8
Rhipicephalus simus	0	0	40	12 (2)	52	8
Argasid ticks	Larvae	Nymphs	Adults		Total	
Ornithodoros porcinus porcinus	0	2	2		4	2

() = Number of maturing female ticks, i.e. the idiosoma of *A. hebraeum* > 9,0 mm and *R. simus* > 6,0 mm
* = Sexes not determined

Arthropods

The total numbers of arthropods recovered from the warthogs in the reserve and on the base are summarised in Tables 3 and 4.

The warthogs harboured 3 flea species, 1 louse species 8 ixodid tick species and 1 argasid tick species. The animals in the reserve not only harboured a greater variety but also greater numbers of parasites than the animals on the base.

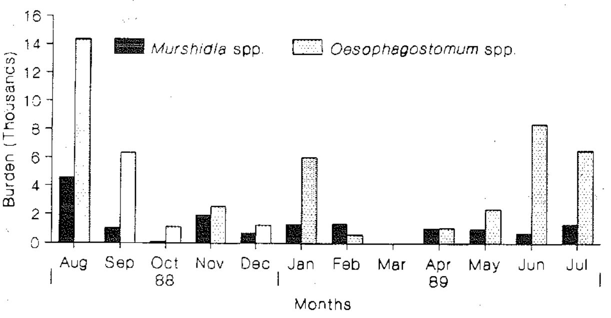

FIG. 2 Seasonal fluctuation in the numbers of *Oesophagostomum* spp. and *Murshidia* spp. in warthogs in the reserve

The seasonal abundance of the adults of the tick *Rhipicephalus simus*, the fleas *Echidnophaga inexpectata* and *Echidnophaga larina* combined and the louse *Haematopinus phacochoeri* for both groups of warthogs are graphically illustrated in Fig. 5–7. Because of the large variation in the burdens of the lice, the burdens have been transformed to their square roots (Fig. 7).

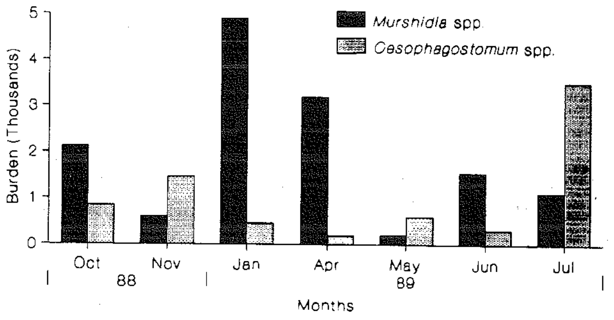

FIG. 3 Seasonal fluctuation in the numbers of *Oesophagostomum* spp. and *Murshidia* spp. in warthogs on the military base

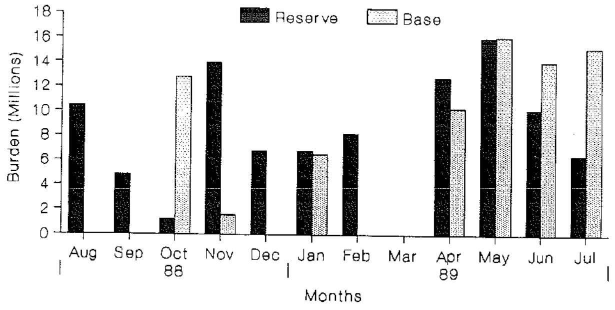

FIG. 4 Seasonal fluctuation in the numbers of *Probstmayria vivipara* in warthogs in the reserve and the military base

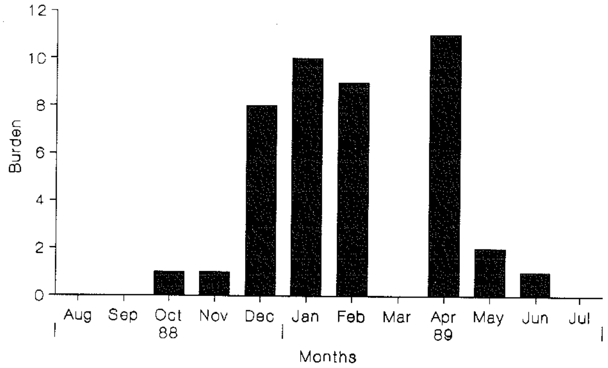

FIG. 5 Seasonal fluctuation in the numbers of *Rhipicephalus simus* on warthogs in the Hoedspruit Nature Reserve

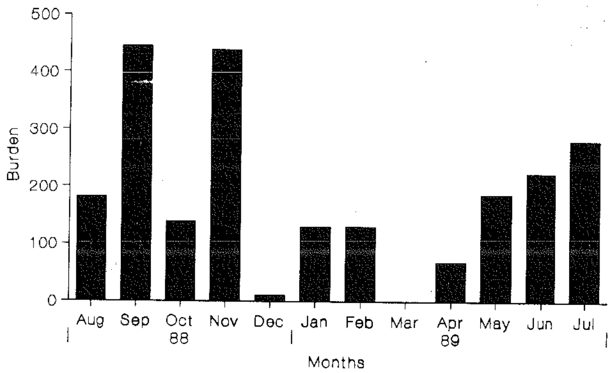

FIG. 6 Seasonal fluctuation in the numbers of *Echidnophaga* spp. on warthogs in the Hoedspruit Nature Reserve

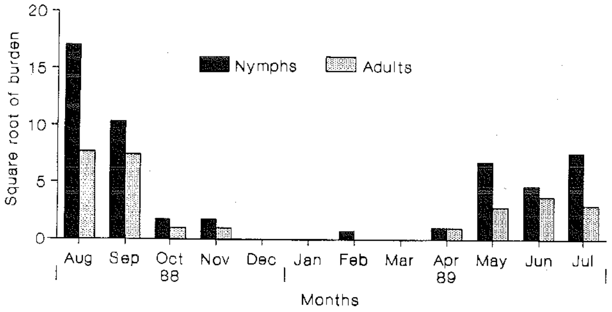

FIG. 7 Seasonal fluctuation in the numbers of *Haematopinus phacochoeri* on warthogs in the Hoedspruit Nature Reserve.

Although variation was considerable, peak flea burdens were generally recorded from August to November and May to July, while peak burdens of immature and adult *H. phacochoeri* were present during August and September. No lice were recovered during December and January. Adult *R. simus* were present from October to June, with the largest numbers being recovered from December to April. The other ectoparasites did not exhibit clear patterns of seasonal abundance.

DISCUSSION

Helminths

Fourteen helminth species were recovered in this study from the warthogs in the reserve. This is 5 species fewer than from warthogs in the KNP, but 4 more than from warthogs in Namibia (Horak, Biggs, Hanssen & Hanssen, 1983; Horak *et al.*, 1988). At least 9 helminths species were recovered from the animals on the base.

The small number of species recovered from warthogs on the base is probably firstly due to the fact that they are an isolated population, consisting of about 80 animals, that has no contact with other warthogs, and secondly because very few other animals species occur on the base. Thus, if cross-infection does take place it can only occur to a limited degree. Neither the carnivore associated *Taenia* sp. and *Echinococcus* sp. larvae, nor *Cooperia hungi, Impalaia tuberculata* or the *Trichostrongylus* spp. were recovered from these warthogs, although they were present in those in the reserve.

The difference in the mean total adult nematode burdens between the 2 groups of warthogs is presumably also due to the above-mentioned factors.

Ascaris phacochoeri, which we consider a definitive parasite of warthogs, has previously been recorded from warthogs from Zululand (Ortlepp, 1939, 1964) and the KNP (Horak *et al.,* 1988). The mean adult burden of the warthogs from the reserve was approximately double that of those in the KNP, while that of the warthogs from the base was about the same (Horak *et al.,* 1988). Only 1 immature *Ascaris* sp. was recovered from the warthogs from Namibia (Horak, Biggs, Hanssen & Hanssen, 1983).

C. hungi is a common parasite of impala, *Aepyceros melampus* (Horak, 1978b). Although the spicules of the specimens recovered during this survey were of normal size, the fact that they were present in only 1 animal confirms their status as an accidental parasite of warthogs. This assumption is augmented by the fact that although large numbers of impala occur in the area in the KNP where warthogs were previously surveyed, *C. hungi* was not found in a single warthog (Horak *et al.,* 1988).

All the *I. tuberculata* recovered in this survey were considerably smaller and the males' spicules shorter than those in antelope (Boomker, 1977; Gibbons, Durette-Desset & Daynes, 1977). This agrees with the findings of Horak *et al.* (1988) for *I. tuberculata* from warthogs in the KNP and those of Horak, Biggs, Hanssen & Hanssen (1983) for *Impalaia nudicollis* from warthogs in Namibia. It indicates that both *Impalaia* species can survive in warthogs but that these animals are not preferred hosts.

Worms of the genus *Murshidia* were not recovered from warthogs in Mozambique or Namibia (Ortlepp, 1964; Horak, Biggs, Hanssen & Hanssen, 1983). Two species of this genus were, however, present in warthogs in the Central African Republic (Troncy, Graber & Thal, 1972), Zululand (Daubney, 1923; Ortlepp, 1964), on the escarpment of the eastern Transvaal and in the eastern Transvaal Lowveld (Ortlepp, 1964; Horak *et al.,* 1988). Only

Murshidia hamata was present in a warthog from the north-western Transvaal (Boomker & Horak, unpublished data, 1989). Horak *et al.* (1988) found large numbers of *Murshidia* spp. in warthogs in the KNP but only moderate numbers were recovered during this survey.

It appears that certain individuals harbour large numbers of *Oesophagostomum* spp. or *Murshidia* spp. but the factors predisposing to such burdens are not known.

With the exception of *Oesophagostomum santosdiasi,* which was recovered from only 1 warthog in the KNP (Horak *et al.,* 1988), the same *Oesophagostomum* spp. as those in the KNP were present in warthogs in this survey. *Oesophagostomum mwanzae* appears to have a very wide distribution and has been recovered from warthogs in the Central African Republic (Troncy *et al.,* 1972), in Uganda, Kenya, Tanzania and Malawi (Daubney 1924; Goodey, 1924), in northern Mozambique and on the escarpment of the eastern Transvaal (Ortlepp, 1964), in the eastern Transvaal Lowveld (Horak *et al.,* 1988), in the north-western Transvaal (Boomker & Horak, unpublished data, 1989) and in northern Namibia (Horak, Biggs, Hanssen & Hanssen, 1983). In the survey of warthogs in Namibia it was outnumbered by *Oesophagostomum mpwapwae* and in the eastern Transvaal Lowveld by *Oesophagostomum mocambiquei.* The latter worm has only been recorded from warthogs on the eastern side of the continent, namely northern Mozambique (Ortlepp, 1964) and the eastern Transvaal escarpment and Lowveld (Ortlepp, 1964; Horak *et al.,* 1988; present survey).

The largest number of *Oesophagostomum* spp. recovered from a single warthog in the present survey was 35 000 worms. This is 4 490 more than recovered from a single animal in Namibia (Horak, Biggs, Hanssen & Hanssen, 1983) and 27 600 more than from an animal in the KNP (Horak *et al.,* 1988). As is apparent from the various surveys, burdens of nematodes of this genus may vary considerably.

From Fig. 1a & 2 it seems that peak numbers of *Oesophagostomum* spp. occurred in warthogs in the reserve approximately 3 months after good rainfall, and that the size of the peak depends on the amount of rain. During October 1988 approximately 30 mm rain fell and a small peak occurred during January 1989. Rainfall in excess of 100 mm was measured during February 1989 and 98 mm during March 1989. Small numbers of *Oesophagostomum* spp. were recovered during May 1989 but a peak was reached during June 1989. No such pattern was, however, seen in the warthogs on the base, nor was it apparent for the *Murshidia* spp. or *Probstmayria vivipara* in both groups of warthogs.

Physocephalus sexalatus occurs in warthogs, bushpigs and domestic pigs in South Africa (Ortlepp, 1964, Horak, 1978a; Reinecke, 1983; Horak *et al.,* 1988). The numbers of *Physocephalus sexalatus* recovered during this survey are similar to those in warthogs in Namibia, but are considerably greater than those in warthogs in the KNP. Contrary to the findings of Horak *et al.* (1988), no seasonal pattern of abundance was evident in this survey.

The related *Ascarops strongylina* has been recorded from bushpigs in the northern Transvaal (Ortlepp, 1964) and domestic pigs (Horak, 1978a) but has as yet not been recorded from warthogs.

As in the case of the warthogs in Namibia and the KNP, *Probstmayria vivipara* occurred in vast numbers and peak burdens were present during the cooler months of the year.

Trichostrongylus deflexus (= *Trichostrongylus colubriformis* of Horak, Biggs, Hanssen & Hanssen, 1983 and *Trichostrongylus instabilis* of Horak *et al.,* 1988) is a recently described nematode of several antelope species (Boomker & Reinecke, 1989). It appears to infect a wide range of hosts, but its presence in warthogs should be regarded as accidental.

Trichostrongylus thomasi is an abomasal parasite of a number of antelope species (Round, 1968; Horak, Meltzer & De Vos, 1982; Horak, Brown, Boomker, De Vos & Van Zyl, 1982; Horak, De Vos & Brown, 1983; Boomker, Horak & De Vos, 1986, 1989) and also occurs in the stomach of Burchell's zebra (Scialdo, Reinecke & De Vos, 1982) and warthogs (Horak *et al.,* 1988; present survey). It fills the same niche in wild animals as is occupied by *Trichostrongylus axei* in domestic animals, but should be regarded as an accidental parasite of warthogs.

Since *Moniezia/Paramoniezia* sp. were recovered only from the younger animals, we postulate that immunity against these tapeworms develops after initial infection, similar to that seen in domestic ruminants infected with *Moniezia expansa* (Reinecke, 1983).

Arthropods

The smaller numbers of species and smaller overall numbers of ectoparasites recovered from the warthogs on the military base than from those in the nature reserve are probably due to the same factors affecting their respective helminth burdens, as mentioned earlier.

Only *Echidnophaga larina* was recovered from the warthogs in Namibia (Horak, Biggs, Hanssen & Hanssen, 1983), while the animals in the KNP and the present survey harboured both *Echidnophaga larina* and *Echidnophaga inexpectata* (Horak *et al.,* 1988). As in the case of the KNP warthogs, the 2 flea species could not be counted separately because of their stick-tight habit, and consequently many were counted *in situ.* This also prevented the determination of their sex. Although considerable variation occurred in the monthly mean flea burdens of the warthogs in Namiba, the KNP and the present survey, it would appear as if the largest numbers of fleas are present during the period May or June to November or December.

The mean burdens of *Moeopsylla sjoestedti* on the warthogs in the HNR were higher than those on the warthogs in the KNP (Horak *et al.,* 1988). The warthogs examined in Namibia did not harbour this flea (Horak, Biggs, Hanssen & Hanssen, 1983). No pattern of seasonal abundance was evident and more female than male fleas were recovered.

In Namibia peak burdens of *Haematopinus phacochoeri* were recorded on warthogs in September of 1 year and June the following year (Horak, Biggs, Hanssen & Hanssen, 1983), while in the KNP peak burdens were present from July to September (Horak *et al.,* 1988). The recovery of large numbers of lice during August and September in the present survey confirms the winter to early spring abundance of this species.

The complete absence of lice on the KNP warthogs during January 1981 (Horak *et al.,* 1988) and during December and January in this survey leads one to speculate as to where and in what stage these permanent ectoparasites oversummer. The most likely explanation would seem to be as eggs attached to the hair of the warthogs or loose in the burrows of the animals. It could also be that the piglets, which are generally born during November or December in South Africa (Smithers, 1983), acquire infestation from their dams and ensure the survival of the lice during the summer months. This was indeed so in the KNP where a 1-month old piglet examined during January 1980 was fairly heavily infested compared with the absence of infestation on the other warthogs slaughtered at the same time. The same, however, did not apply in the case of a similarly aged warthog examined during January 1981.

If one excludes the adult ticks of the single warthog in the KNP that carried an exceptionally large burden of *Amblyomma hebraeum,* then the mean burdens for the warthogs examined there were 74 larvae, 59 nymphs and 14 adults (Horak *et al.*, 1988). The mean burden for the warthogs examined in the reserve in the present survey was 6 larvae, 44 nymphs and 12 adults. With the exception of the larval numbers (for which we have no explanation), the mean burdens of the 2 groups of warthogs were thus reasonably similar. These findings confirm that warthogs are one of the preferred hosts of adult ticks of this species. The immature stages, and more particularly the larvae, feed on a large variety of mammals and also one some ground-nesting birds (Theiler, 1962; Horak, MacIvor, Petney & De Vos, 1987). Consequently, the immature stages which feed on warthogs are not solely responsible for generating the adult burdens on the same animals.

The warthogs in Namibia, the KNP and the present survey were infested with adult *Hyalomma truncatum* but burdens were never very large (Horak, Biggs, Hanssen & Hanssen, 1983: Horak *et al.*, 1988). Preferred hosts of the adults are large herbivores such as zebras, eland and cattle (Horak, 1982; Rechav, 1986; Horak & MacIvor, 1987). Scrub hares are preferred hosts of the immature stages, which are also found on rodents (Rechav, 1986: Horak & MacIvor, 1987).

Horak *et al.* (1988) state that in the KNP adult *Rhipicephalus simus* seem to prefer monogastric animals such as Burchell's zebras, carnivores and wart-hogs rather than ruminants. The fairly large numbers of adults recovered from the warthogs in the present investigation confirm their observations for this host species. The immature stages of *R. simus* feed on rodents (Norval & Mason, 1981).

The period of peak adult abundance from December to April corresponds to that of January to April with a peak in February on the warthogs in the KNP (Horak *et al.*, 1988). The mean burden of *R. simus* on the warthogs in that survey was more than double that in the present study.

The larvae of *Amblyomma marmoreum* utilise a large number of mammals and some ground-frequenting birds as hosts (Horak *et al.*, 1987). Their presence on the warthogs, albeit in small numbers, is therefore not unexpected. We consider *Boophilus decoloratus, Rhipicephalus appendiculatus, Rhipicephalus evertsi evertsi* and *Rhipicephalus zambeziensis* to be accidental infestations. Their occurrence on the warthogs probably reflects their periods of peak seasonal abundance rather than host preference.

The presence of *Ornithodoros porcinus porcinus* on warthogs that are out of their burrows has been discussed by Horak *et al.* (1988). Its recovery from warthogs in Namibia, the KNP and the present survey indicates that this must be considered a normal occurrence.

ACKNOWLEDGEMENTS

We thank the South African Defence Force for placing the animals at our disposal, and Messrs D. Breytenbach, P. Oosthuizen, C. du Plessis and J. Botha for assistance with the autopsies. This study was partly funded by the Foundation for Research Development.

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HELMINTH COMMUNITIES

J. Parasitol., 89(5), 2003, pp. 899–907

PATTERNS OF ASSOCIATION, NESTEDNESS, AND SPECIES CO-OCCURRENCE OF HELMINTH PARASITES IN THE GREATER KUDU, *TRAGELAPHUS STREPSICEROS*, IN THE KRUGER NATIONAL PARK, SOUTH AFRICA, AND THE ETOSHA NATIONAL PARK, NAMIBIA

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ABSTRACT: The helminth parasites of the greater kudu from the Kruger National Park (KNP), South Africa, and the Etosha National Park (ENP), Namibia, were examined to determine the major patterns of spatial and demographic variation in community structure and to evaluate nonrandomness in parasite community assembly. Nonmetric multidimensional scaling ordination procedures were used to test for differences in parasite community composition between hosts of the 2 parks and between hosts of different demographic groups within KNP. Infracommunities within KNP were also examined for patterns of nonrandomness using 2 null models, i.e., nestedness and species co-occurrence. Infracommunities of KNP and ENP were significantly different from each other, as were infracommunities of different host demographic groups within KNP. Parasite species in the greater kudu from KNP displayed significant levels of nestedness and were found to co-occur less frequently than expected by chance; however, this lack of co-occurrence was significant only when all demographic groups were considered. When restricted to any particular age class, co-occurrence patterns could not be distinguished from random. Overall, these data suggest that biogeography and host demographics are important factors in determining community organization of helminth parasites in the greater kudu.

One of the key concerns of community ecology is to establish whether species assemblages are structured entities or stochastic groupings and, if structured, what mechanisms are responsible for their organization (Gotelli and McCabe, 2002; Janovy, 2002). A common way to conclude whether an assemblage of species is a structured or ordered community is to determine whether specific groupings of species are associated with a particular habitat or biogeographic area (Brown and Lomilino, 1998), i.e., whether there are observable patterns in the distribution of species (Roberts et al., 2002). Within the context of host–parasite systems, the combination of species assemblages with habitat can be further subdivided by testing for associations among hosts of different genders and age classes. Structured communities can also be delineated by a departure from randomness, where an assemblage of species is significantly more ordered than would be expected by chance. To test whether communities are significantly structured, pattern-based null models are often formulated. These null models are pattern-generating methods that intentionally exclude a mechanism of interest to determine whether a specific pattern can be produced by a stochastic process (Gotelli, 2000, 2001). Two useful null models that have been used to assess community structure are species nestedness (Atmar and Patterson, 1993) and species co-occurrence (Gotelli and McCabe, 2002).

Community nestedness represents a Russian doll-like pattern in which species-poor communities are an ordered subset of more diverse communities (Atmar and Patterson, 1993). Nestedness has been well documented for both free-living (Patterson and Atmar, 1986; Fernandez-Juricic, 2002) and parasitic taxa (Poulin and Valtonen, 2001; Šimková et al., 2001) and has been used extensively to test for nonrandom patterns among species assemblages. Nested patterns were originally thought to develop through ordered extinction (Patterson and Atmar, 1986) but have subsequently been shown to arise through colonization as well (Simberloff and Martin, 1991). Although nestedness can evolve through both colonization and extinction processes, it suggests a higher-level order that renders community structure predictable.

Species co-occurrence models are largely built upon Diamond's (1975) community assembly rules, i.e., forbidden species combinations, checkerboard distributions, and incidence functions (Gotelli and McCabe, 2002), where species are predicted to co-occur less frequently than would be expected by chance alone owing to competitive interactions. Many of Diamond's (1975) original assembly rules have been converted to measurable co-occurrence indices and have been used to determine whether communities lack certain species combinations. One of the more powerful co-occurrence indices is Stone and Roberts' (1990) C-score metric, which is used to measure the average number of ''checkerboard'' units in a species presence–absence matrix. A checkerboard pattern refers to the case where species A is present in a host while species B is absent, combined with the presence of species B in another host where species A is absent. Such a pattern is thought to arise when competitive interactions are important in structuring a community (Diamond, 1975; Gotelli and McCabe, 2002).

The parasites of a wide range of African ruminants have been the subject of extensive surveys (Mönnig, 1932; Boomker, 1982, 1991; Horak et al., 1983; Boomker et al., 1991, 1997). These studies have culminated into several substantial checklists detailing the species present, levels of abundance and prevalence, and insights into seasonal fluctuations (Boomker et al., 1986, 1989). Despite the considerable progress that has been made, there is a dearth of detailed community studies from this region.

To this end, we examined an exceedingly diverse and abundant assemblage of helminths from 119 greater kudus (*Tragelaphus strepsiceros*) from 2 localities in southern Africa. The effort was designed to determine whether (1) parasite communities differ between geographic locations, (2) parasite communities differ between hosts of different age classes or gender, (3) parasite infracommunities form nested subsets, and (4) helminth communities in the greater kudu exhibit evidence of competitive exclusion.

Received 3 February 2003; revised 23 June 2003; accepted 23 June 2003.

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METHODS

Study areas

Kudus were collected from the southern part of the Kruger National Park (KNP) in South Africa and the Etosha National Park (ENP) in Namibia. The KNP is a 19,485-km^2 park located in the northeast portion of South Africa. The vegetation in the southern region of KNP is relatively diverse, consisting of 4 veld types (Boomker et al., 1989). The climate varies from warm or hot summers to mild winters, with an annual rainfall between 600 and 700 mm. The ENP is a 22,269-km^2 reserve located in the northern region of Namibia. The ENP is centered on the Etosha salt pan in a semiarid habitat with an annual rainfall around 389 ± 118 mm (Simmons, 1996). Vegetation consists largely of desert scrub and mopane forests.

Study animals

The greater kudu, *T. strepsiceros*, is a large antelope, reaching upwards of 315 kg, and is distributed widely throughout southern and eastern Africa. Kudus are consummate browsers, feeding primarily on flowers, fruits, seeds, pods, leaves, and twigs of a variety of plants, but they seldom consume grass (Owen-Smith and Cooper, 1987; Boomker et al., 1989). Social organization is based on the cow social unit, where a closed matriarchal kinship group consisting of several cows and their offspring is formed. Calves stay concealed for the first 3 mo of their lives before joining the maternal group (Boomker et al., 1989). Males leave the maternal group at approximately 2 yr of age and form temporary associations with peers. Adult bulls show a tendency to become increasingly solitary with age and form transient associations with cows during the breeding season.

Data collection

A total of 119 kudus were collected from KNP and ENP. Ninety-six kudus were taken from KNP between April 1981 and March 1983 as part of a previous survey (Boomker et al., 1989). In brief, monthly collections from KNP included 1 adult male, 1 adult female, 1 young adult male, and 1 juvenile or calf of either sex. Full-body necropsies of these animals were performed, and all helminths were identified and counted. Twenty-three kudus were culled from ENP on a bimonthly basis from June 1983 to April 1984. Two adult males and 2 adult females were taken on each occasion. Necropsies were performed using the same procedures as those used in KNP.

Data analysis

Nonmetric multidimensional scaling (NMDS) was used to elucidate differences in community structure between KNP and ENP. NMDS has been used extensively in free-living ecology to examine the associations of species assemblages with different habitats (Bailey and Whitham, 2002), and it has also been used to examine differences in parasite communities along a stream gradient in Appalachian fishes (Barger and Esch, 2001). Ordinations were performed using 2 separate distance matrices, one constructed from quantitative abundance data using the Sorenson distance measure and the other created from presence–absence data also using Sorenson distance. Sorenson distance was used for distance matrices because it is well suited for both quantitative data and presence–absence data (McCune and Medford, 1999). Differences in community composition between KNP and ENP were analyzed using multiresponse permutation procedures (MRPP). An indicator species analysis that calculates species indicator values (IV) was used to determine which species differed between the 2 parks. This analysis was used because it combines both abundance and prevalence data to determine whether a particular species is indicative of a given habitat (McCune and Medford, 1999). Ordination procedures, MRPP, and indicator species analyses were all performed using PC-ORD software (McCune and Medford, 1999).

Differences in parasite community composition among hosts of different age classes and genders were examined using NMDS, MRPP, and indicator species analyses. No difference was detected between male and female hosts and between juvenile and adult hosts. Subsequently, male and female hosts and adults and juveniles were lumped together for all the remaining analyses. A Kruskal–Wallis test was performed to test for differences in species richness among different age-class hosts.

The presence of nested communities was examined using Nested Calculator software (Atmar and Patterson, 1995) to compare the degree of nestedness in kudu infracommunities from KNP, with the level of nestedness from 1,000 randomly generated communities based on presence–absence data from KNP. The level of significance was determined by calculating the frequency of randomly generated communities that contained greater levels of nestedness.

A co-occurrence module developed by Gotelli and Entsminger (1999) was used to determine whether parasite species co-occurred less frequently than expected by chance. This module was performed using the C-score index of Stone and Roberts (1990), which measures the average number of checkerboard units among all possible combinations of species and has been shown to be resistant to type I error (Gotelli, 2002). This model was run 4 different times using data from KNP for the following scenarios: (1) for all helminths of all kudus, (2) for all helminths of adults only, (3) for enteric nematodes of all kudus, and (4) for enteric nematodes of adults only. Each of the observed C-score values was compared with C-score values for 5,000 randomly generated matrices to establish significance.

RESULTS

Twenty-two species of helminths were recovered from 96 kudus in KNP. Of these, 16 species were nematodes, 4 cestodes, and 2 trematodes (Tables I–III). Eleven of the 16 species of nematodes were trichostrongylids. Four of the 16 nematode species were common, infecting more than 50% of the hosts. Three were of intermediate prevalence, infecting more than 10% of the hosts but less than 50%, whereas the remaining 9 nematode species were rare, infecting less than 10% of the kudus from KNP. The 2 trematodes from KNP, *Schistosoma mattheei* and *Calicophoron* sp., had intermediate levels of prevalence, whereas 3 of the 4 cestode species infected less than 10% of the hosts; *Taenia* sp. infected 11% of the kudus from KNP.

Thirteen species of helminths were recovered from 23 kudus in ENP, including 11 species of nematodes and 2 cestodes (Tables IV, V). Nine of the 11 nematode species were trichostrongylids. Only 2 species from ENP, *Cooperia neitzi* and *Haemonchus vegliai*, infected more than 50% of the hosts. Five species were intermediate in abundance, whereas the remaining 6 (including the 2 cestode species) were rare, infecting <10% of the hosts.

Quantitative abundance ordination of kudu infracommunities from both KNP and ENP explained 79% of the variation in these data (axis 1 = 48%, axis 2 = 31%, stress = 0.11) and displayed a high level of segregation in ordination space between hosts from different geographic locations (Fig. 1A). A 2-dimensional ordination solution based on presence–absence data revealed similar results, explaining 84% of the variation among infracommunities (stress = 0.20) and suggesting even greater levels of infracommunity segregation between KNP and ENP with almost no overlap in ordination space (Fig. 1B). MRPP were performed to test the hypothesis that there is no difference in parasite community composition between KNP and ENP. This hypothesis was rejected for both quantitative ($P < 0.0001$; A = 0.08) and presence–absence data ($P < 0.0001$; A = 0.06). Further examination of the 2 component communities showed significant differences in the indicator values (a metric of abundance and prevalence combined) of 10 species between the 2 parks (Table VI). Six parasite species were found to be more commonly associated with kudus from KNP, whereas 4 species were more indicative of kudus from ENP. The indicator value for *S. mattheei*, which occurs only in KNP, was not statistically significant ($P = 0.07$: IV = 20.8); however, the

TABLE I. Mean abundance (±SE), prevalence, and trait matrix for nematode species recovered from 96 kudus from the Kruger National Park.

Nematodes	Abundance	Prevalence	Transmission	Site	Family
*Haemonchus vegliai**	122.5 ± 137.5	88	Ingestion	GI tract†	Trichostrongylidae
*Cooperia neitzi**	502.8 ± 578.7	83	Ingestion	GI tract	Trichostrongylidae
*C. acutispiculum**	120.9 ± 144.2	77	Ingestion	GI tract	Trichostrongylidae
*Elaeophora sagittus**	10.8 ± 21.6	68	Vector	PA and CBV‡	Onchocercidae
*Trichostrongylus deflexus**	106.3 ± 254.6	44	Ingestion	GI tract	Trichostrongylidae
Agriostomum gorgonis§	9.3 ± 25.5	28	Penetration, vertical	GI tract	Chabertiidae
Impalaia tuberculata§	21.5 ± 82.9	22	Ingestion	GI tract	Trichostrongylidae
T. falculatus‖	4.7 ± 15.9	10	Ingestion	GI tract	Trichostrongylidae
C. hungi‖	6.8 ± 29.6	8	Ingestion	GI tract	Trichostrongylidae
Strongyloides papillosus‖	46.8 ± 283.1	6	Penetration, vertical	GI tract	Strongyloididae
Trichuris sp.‖	1.3 ± 5.6	5	Ingestion	GI tract	Trichuridae
C. fuelleborni‖	1.6 ± 9.5	4	Ingestion	GI tract	Trichostrongylidae
Paracooperia devossi‖	0 ± 0.1	2	Ingestion	GI tract	Trichostrongylidae
Setaria sp.‖	0 ± 0.1	2	Vector	Body cavity	Onchocercidae
C. yoshidai‖	0.5 ± 5.1	1	Ingestion	GI tract	Trichostrongylidae
Parabronema sp.‖	0 ± 0.1	1	Vector	GI tract	Habronematidae

* Common species infecting more than 50% of the host population.
† Gastrointestinal tract.
‡ Pulmonary artery and coronary blood vessels.
§ Occasional species infecting more than 10% but less than 50% of the host population.
‖ Rare species infecting less than 10% of the host population.

parasite was found to be statistically more prevalent in KNP ($\chi^2 = 0.99$; $P < 0.001$).

An MRPP analysis of hosts from different age classes within KNP revealed significant differences in community composition between calves and adults ($P < 0.0001$; A = 0.06) and between calves and juveniles ($P = 0.0003$; A = 0.07); however, there was no significant difference between adults and juveniles ($P = 0.15$; A = 0.007). These differences are readily apparent in ordination space based on quantitative (stress = 0.11) (Fig. 2A) and presence–absence (stress = 0.17) (Fig. 2B) matrices. Both quantitative and presence–absence ordination solutions show a high level of segregation for parasites in calves from those in adults and juveniles, whereas those in adults and juveniles largely cluster together. Because there was no detectable difference in parasite community composition between adults and juveniles, these 2 age classes were lumped together, and a species indicator analysis was performed to test for associations between individual species and specific age-class hosts. Twelve species, all nematodes, were found to be indicative of a particular age-class host (Table VII). Six species were more commonly associated with adults and juveniles, and 6 species were more commonly associated with calves. Furthermore, a Kruskal–Wallis test was performed to determine whether there were differences in parasite species richness among different age-class hosts. This analysis returned a significant *P* value ($P = 0.01$), with adult kudus harboring the greatest number of species, juveniles the second greatest number of species, and calves the least number of species.

An examination of 2 community null models revealed highly nonrandom patterns of parasite infracommunity structure within KNP kudus. Kudu infracommunities were significantly nested ($P < 0.0001$; Fig. 3), demonstrating that rare species primarily occur in more diverse infracommunities. A comparison of observed C-score indices with C-score values from randomly generated communities exposed a lack of species co-occurrence for all helminths ($P = 0$; C-score = 92.1) and for enteric nematodes ($P = 0$; C-score = 109.6) when all kudus from KNP were examined (Table VIII). When this co-occurrence null model was restricted to a specific age class, including adults from ENP, parasite species were distributed randomly with respect to co-occurrence patterns (Table VIII).

DISCUSSION

The greater kudu parasite communities from KNP and ENP are species rich and abundant. Both communities are largely composed of enteric nematodes primarily from the Trichostrongylidae. *Haemonchus veglia*, *C. neitzi*, and *C. acutispiculum* were the 3 most abundant helminths in both KNP and ENP. It is unclear why these worms are more common then other helminths in this system. However, Horak (1980) and Boomker et al. (1989) have suggested that kudus in KNP serve as the pri-

TABLE II. Mean abundance (±SE), prevalence, and trait matrix for trematode species recovered from 96 kudus from the Kruger National Park.

Trematodes	Abundance	Prevalence	Transmission	Site	Family
Calicophoron sp.*	31.8 ± 92.7	32	Ingestion	GI tract†	Paramphistomatidae
*Schistosoma mattheei**	3.9 ± 11.3	20	Penetration	Blood vascular system	Schistosomatidae

* Occasional species infecting more than 10% of the host population.
† Gastrointestinal tract.

TABLE III. Mean abundance (±SE), prevalence, and trait matrix for cestode species recovered from 96 kudus from the Kruger National Park.

Cestodes	Abundance	Prevalence	Transmission	Site	Family
Taenia sp*	0.2 ± 0.9	11	Ingestion	Muscle	Taeniidae
*Moniezia benedeni**	0.2 ± 0.7	10	Ingestion	GI tract†	Anoplocephalidae
Avitellina sp*	0.1 ± 0.7	3	Ingestion	GI tract	Anoplocephalidae
Echinococcus sp.*	0 ± 0.1	1	Ingestion	Liver	Taeniidae

* Rare species infecting less than 10% of the host population.
† Gastrointestinal tract.

mary definitive host for these worms along with *Trichostrongylus deflexus*. Many of the other species found in this study are probably maintained commonly in other ungulate, or herbivorous, hosts, only occasionally or rarely infecting kudus.

The segregation of kudu infracommunities of different geographic locations in ordination space suggests strong differences in component parasite community structure between kudus from the 2 parks. This contention is further supported by the MRPP results, which revealed that kudu infracommunities of KNP and ENP were compositionally distinct, i.e., parasite communities within a park are more similar to each other than to parasite communities from the other park. These data also confirm the results demonstrated by Goüy de Bellocq et al. (2002), who examined parasite communities of 16 species of mammals and found parasites to be a reliable biogeographic marker. It is likely that these disparities stem from major differences in climate and vegetation between the 2 parks, as well as slight differences in the ungulate fauna and the absence of the required intermediate snail hosts in ENP. Thus, ENP is generally considered as semiarid, and the vegetation consists largely of desert scrub in the south and mopane forests in the north. KNP tends to be a wetter region of southern Africa, with an annual rainfall of 600–700 mm/yr and a more diverse flora (Boomker et al., 1989). The ungulate faunas of the 2 parks are relatively similar, although there are some slight differences. For example, springbok and gemsbok are not present in KNP but occur in ENP, whereas, buffalo, oribi, and grysbok are absent from ENP but present in KNP. It is possible that the presence or absence of these potential host species could influence the transmission dynamics for a number of the generalist parasites.

Another important difference between the 2 parks is the absence of *Bulinus globosus* in ENP (K. de Kock, pers. comm.). The absence of this snail explains the lack of *S. mattheei* in ENP. Even though 2 closely related species, *B. forskali* and *B. angolensis*, both occur in Etosha, there is no report of natural infection of *S. mattheei* in ENP. The absence of *Onchocerca* sp. in KNP is perplexing because the vectors for this parasite, *Simulium* spp., are abundant in the park (E. Nevill, pers. comm.). It is possible that *Onchocerca* sp. could be absent from KNP because of historical factors; however, it seems reasonable that it could easily spread throughout the range of *Simulium* spp. in Africa, and thus it is likely that there are unknown abiotic factors preventing the transmission of *Onchocerca* sp. in KNP. Further studies are needed to establish the factors limiting the range of *Onchocerca* sp. in southern Africa.

Within KNP, host demographics appear to be a reliable predictor of infracommunity structure. Both quantitative and presence–absence ordination solutions displayed a strong separation of calf infracommunities from juvenile and adult infracommunities. This segregation of calves from juvenile and adult infracommunities in ordination space was confirmed using an MRPP analysis, demonstrating that calf infracommunities are compositionally distinct from those of adults and juveniles. The factor driving this difference in community composition is not solely an accumulation of parasites associated with age but rather that 6 species are more commonly associated with calves and 6

TABLE IV. Mean abundance (±SE), prevalence, and trait matrix for nematode species recovered from 23 kudus from the Etosha National Park.

Nematodes	Abundance	Prevalence	Transmission	Site	Family
*Cooperia neitzi**	88 ± 113.8	68.4	Ingestion	GI tract†	Trichostrongylidae
*Haemonchus vegliai**	26 ± 29.4	63.2	Ingestion	GI tract	Trichostrongylidae
C. acutispiculum‡	63 ± 120.3	47.4	Ingestion	GI tract	Trichostrongylidae
Onchocerca sp.‡	1 ± 1.7	47.4	Vector	Conn. tissue§	Onchocercidae
Cooperiodes hamiltoni‡	8 ± 18.7	21.1	Ingestion	GI tract	Trichostrongylidae
Impalaia nudicollis‡	9 ± 22.4	15.8	Ingestion	GI tract	Trichostrongylidae
Trichostrongylus thomasi‡	4 ± 12.5	10.5	Ingestion	GI tract	Trichostrongylidae
Paracooperia devossi‖	11 ± 45.9	5.3	Ingestion	GI tract	Trichostrongylidae
Elaeophora sagittus‖	0 ± 0.5	5.3	Vector	PA and CBV#	Onchocercidae
I. tuberculata‖	3 ± 11.5	5.3	Ingestion	GI tract	Trichostrongylidae
T. falculatus‖	1 ± 5.7	5.3	Ingestion	GI tract	Trichostrongylidae

* Common species infecting more than 50% of the host population.
† Gastrointestinal tract.
‡ Occasional species infecting more than 10% but less than 50%, of the host population.
§ Connective tissue.
‖ Rare species infecting less than 10% of the host population.
\# Pulmonary artery and coronary blood vessels.

TABLE V. Abundance (±SE), prevalence, and trait matrix for cestode species recovered from 23 kudus from the Etosha National Park.

Cestode	Abundance	Prevalence	Transmission	Site	Family
*Moniezia expansa**	0 ± 0.2	5.3	Ingestion	GI tract†	Anoplocephalidae
*Thysaniezia giardi**	0 ± 0.2	5.3	Ingestion	GI tract	Anoplocephalidae

* Rare species infecting less than 10% of the host population.
† Gastrointestinal tract.

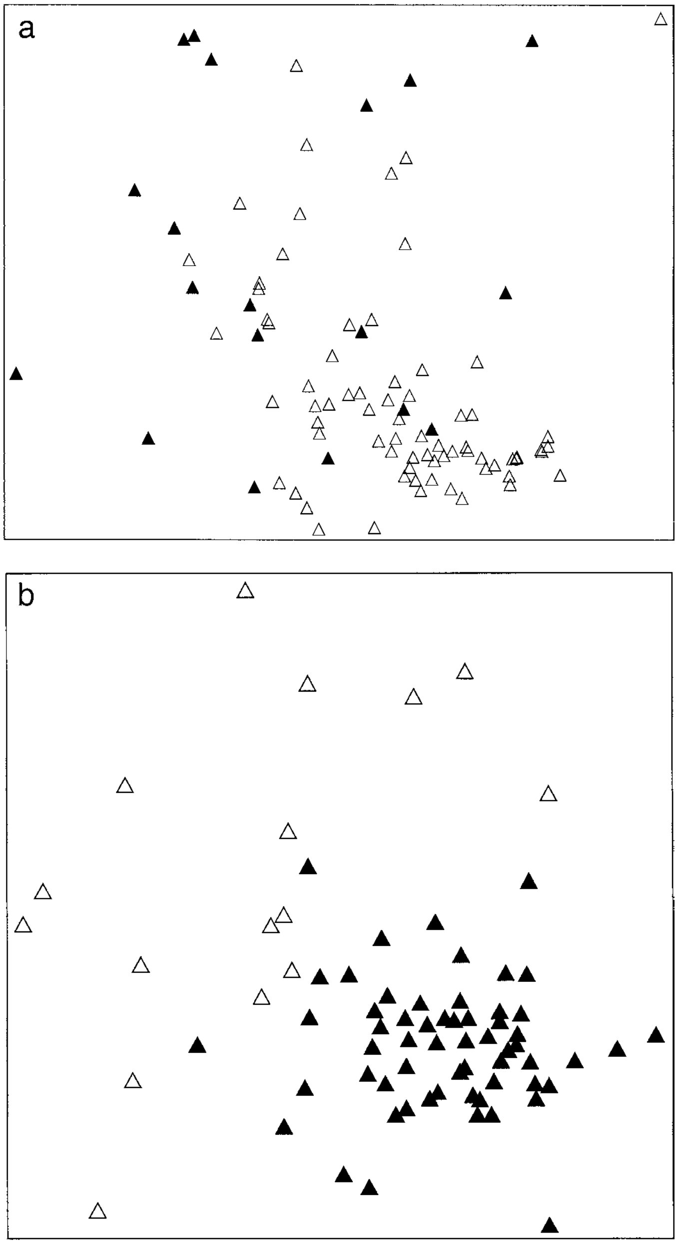

FIGURE 1. Nonmetric multidimensional solutions for kudu infracommunities from Kruger and Etosha National Parks (KNP and ENP, respectively) based on (**A**) quantitative abundance data (axis 1 = 48%, axis 2 = 31%, stress = 0.11) and (**B**) presence–absence data (axis 1 = 34%, axis 2 = 50%, stress = 0.20). △ and ▲ = infracommunities from KNP and ENP National Parks, respectively.

other species are more common in adult or juvenile hosts. Five trichostrongylids, as well as *Strongyloides papillosus*, were found to be significantly more indicative of calf hosts than of any other demographic group. Several explanations are possible for the increased ‘‘association’’ with calves. Calves are still undergoing an experimental learning period, when they are likely to eat any vegetation that is present, including grass, whereas adults are consummate browsers, rarely grazing on grass. Because transmission of these trichostrongylid species requires the ingestion of grass to which infective larvae adhere, calves would have a greater exposure and, therefore, opportunity to recruit larval parasites. Density-dependent mechanisms, such as acquired immunity and parasite-induced host mortality, are also potential factors that could be important in generating the differences between calf infracommunities and those of adults and juveniles. Explanatory models elucidating the aggregation of trichostrongylid infections in ruminant hosts have attributed similar patterns to the density-dependent effects of acquired immunity and parasite-induced host mortality (Grenfell et al., 1995). Acquired host resistance has been well documented for several trichostrongylid species (Reinecke, 1983), and, as such, many of these infections may be maintained through immunologically naive hosts. The greater occurrence and abundance of *S. papillosus* in calves may be due to the vertical transmission of the parasite, even though this parasite may also be acquired via a percutaneous route or by direct ingestion of L3 stages. Because *S. papillosus* may be transmitted by the transmammary route (Moncol and Grice, 1974), an infected mother could pass the parasite infection to all her offspring.

The greater association of the 6 parasite species in adult hosts can be attributed to differences in behavior as well as increased exposure of parasites over time. Presumably, adult kudus have greater overall energy demands and spend more time feeding. Further, calves remain hidden from the maternal group for the first few months of their lives, resulting in a differential exposure to parasites. Finally, by chance alone, adults are likely to be exposed to a wider array of parasites over time and will likely accumulate new, but rare, parasite species throughout their lives. This pattern has been well documented in many other host–parasite systems (Esch and Fernandez, 1993). Similarly, Poulin (1997) has reviewed major patterns of parasite species richness and has documented a positive correlation between parasite species richness and host geographic range for several rodent species, suggesting that vagile species will tend to acquire more parasites and parasite species. Because adult kudus are more mobile than calves, they will be exposed to more parasites not only as a function of time but also as a function of space.

Nested analyses of kudu data from KNP displayed a highly ordered distribution of parasite species among kudu infracom-

TABLE VI. Parasite species indicative of Kruger and Etosha National Parks (KNP and ENP, respectively).

KNP			ENP		
Species	IV†	*P* value	Species	IV†	*P* value
*Cooperia acutispiculum**	65.9	0.001	*Cooperiodes hamiltoni*	21.1	0.003
*C. neitzi**	80.3	0.001	*Impalaia nudicollis*	15.8	0.009
*Elaeophora sagitta**	86.9	0.001	*Onchocerca* sp.	47.4	0.001
*Haemonchus vegliai**	79.2	0.001	*Trichostrongylus thomasi*	10.5	0.033
T. deflexus	33.3	0.022			
Calicophoron sp.	40.3	0.015			

* Parasite species recovered in both KNP and ENP.
† IV = observed species indicator value.

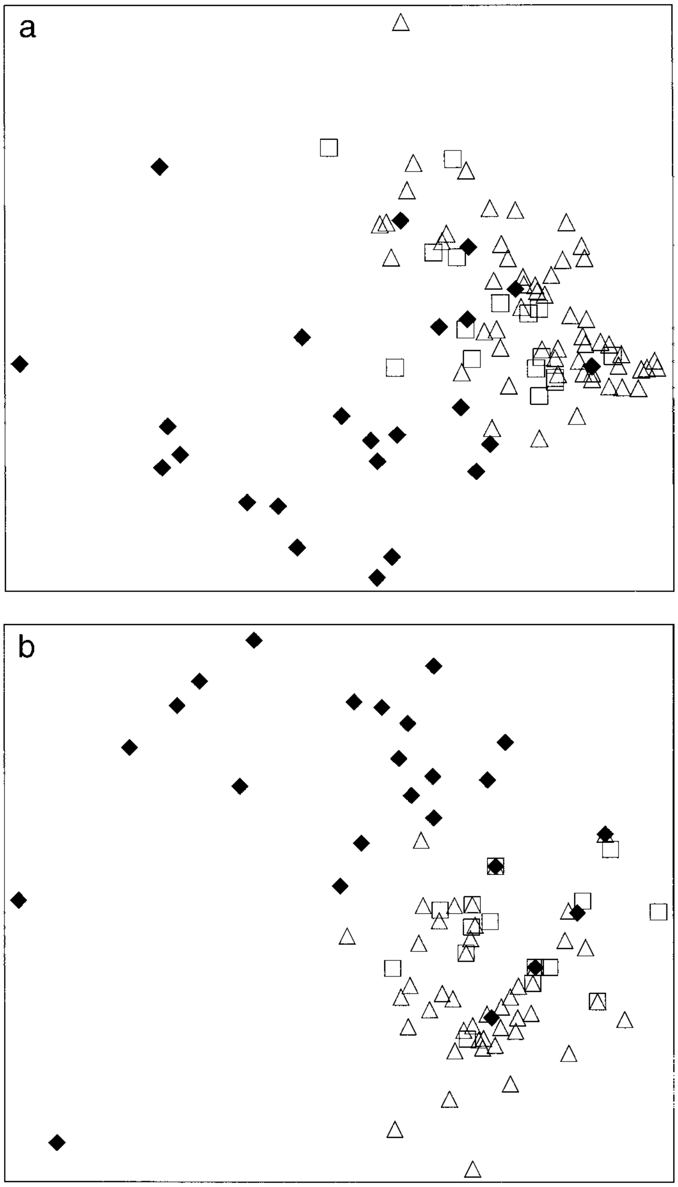

FIGURE 2. Nonmetric multidimensional solutions for adult and calf kudu infracommunities based on (**A**) quantitative data (axis 1 = 44%, axis 2 = 27%, stress = 0.11) and (**B**) presence–absence data (axis 1 = 59%, axis 2 = 30%, stress = 0.17). △ = adult infracommunities, □ = juvenile infracommunities, ◆ = calf infracommunities.

munities. A nested pattern implies a hierarchical community structure, where species-poor infracommunities represent an ordered subset of more diverse communities. Moreover, nestedness suggests that rare species are likely to be found in only the most diverse communities. Several explanations have been proposed for nested patterns for free-living organisms (Atmar and Patterson, 1993) as well as for parasites (Poulin and Valtonen, 2001). An ordered extinction of species due to low population density of species-poor patches has been proposed for nestedness among insular mammal communities, but it is not a feasible explanation for most parasites because of varied indirect life cycles and metapopulation dynamics (Guégan and Hugueny, 1994). Other hypotheses that have been put forth to explain nested subsets include (1) positive interactions, where the presence of one species facilitates the presence of another, either through suppresion of the host's immune response or through an alteration of the host–parasite in such a way as to make recruitment of another species more conducive; (2) increased habitat heterogeneity, where there is a positive association between niche diversification and host size or age; and (3) passive sampling of parasites by the host, where hosts are exposed to a greater diversity of species over time by chance alone (Guégan and Hugueny, 1994). Although these hypotheses are not necessarily mutually exclusive and are difficult, if not impossible, to distinguish from each other by observation alone, the passive sampling hypothesis appears to be the most parsimonious explanation. A comparison of species richness values between different age classes is consistent with this hypothesis, where adult kudus were found to harbor the greatest number of species, juveniles the second greatest number of species, and calves the least number of species. Whereas experimental studies are needed to tease apart the various hypotheses generating nestedness in this system, the fact that kudu infracommunities form a nested pattern is central to understanding the patterns for commonness and rarity among ungulate parasites.

The lack of co-occurrence observed among all helminth species, and among species of enteric nematodes in KNP, is likely the result of age-related differences in hosts and not of competitive exclusion. Patterns of species co-occurrence, i.e., checkerboard distributions, are often regarded as evidence for competitive exclusion (Diamond, 1975; Gotelli and McCabe, 2002); however, in the present study, significant C-score values were obtained only when hosts of all age classes were examined. When these analyses were restricted to any particular age group, they were found to occur randomly with regard to com-

TABLE VII. Parasite species indicative of adult or calf hosts.

Adults			Calves		
Species	IV*	*P* value	Species	IV*	*P* value
Agriostomum gorgonis	36.0	0.006	*Cooperia fuelleborni*	16.7	0.003
C. acutispiculum	80.0	0.001	*C. hungi*	28.8	0.001
C. neitzi	75.2	0.001	*Impalaia tuberculata*	32.7	0.006
Elaeophora sagitta	85.7	0.001	*Strongyloides papillosus*	20.8	0.001
Haemonchus vegliai	73.4	0.001	*Trichostrongylus deflexus*	64.0	0.001
Calicophoron sp.	35.1	0.001	*T. falculatus*	22.2	0.004

* IV = observed species indicator value.

petitive exclusion. Similarly, when the data matrix of kudus from ENP, which contained only adults, was examined for checkerboard distributions, the lack of co-occurrence was not detected. These results support the findings of Gotelli and Rohde (2002), who examined checkerboard patterns in the ectoparasite communities of marine fishes and found largely random co-occurrence patterns. They surmised that the life history characteristics of many parasites, i.e., small size and limited vagility, have prevented the saturation of ecological niches, and as a consequence, the interspecific interaction of parasites remains a rare phenomenon.

Although the nonrandom co-occurrence patterns found in this study are unlikely to be the result of competitive exclusion, this does not diminish their importance but rather serves to illustrate that parasite species in the greater kudu from KNP are segregated in ecological time. D. P. Pielou and E. C. Pielou (1968) and Gotelli and Rohde (2002) noted that nonrandom co-occurrence patterns can arise in the absence of competition if there exists a level of site–host heterogeneity. These authors also warned that it is difficult, and often impossible, to distinguish between these 2 alternative hypotheses; however, the examination of co-occurrence patterns within, and among, different age-class hosts allows for a distinction between these 2 hypotheses. In the present study, it has been demonstrated that calf infracommunities harbor parasite assemblages that are compositionally distinct from those of adults and juveniles. It is therefore reasonable to suspect that the checkerboard distribution of parasites among all age classes is the result of differential associations of parasites with specific age-class hosts and not of a competitively structured community.

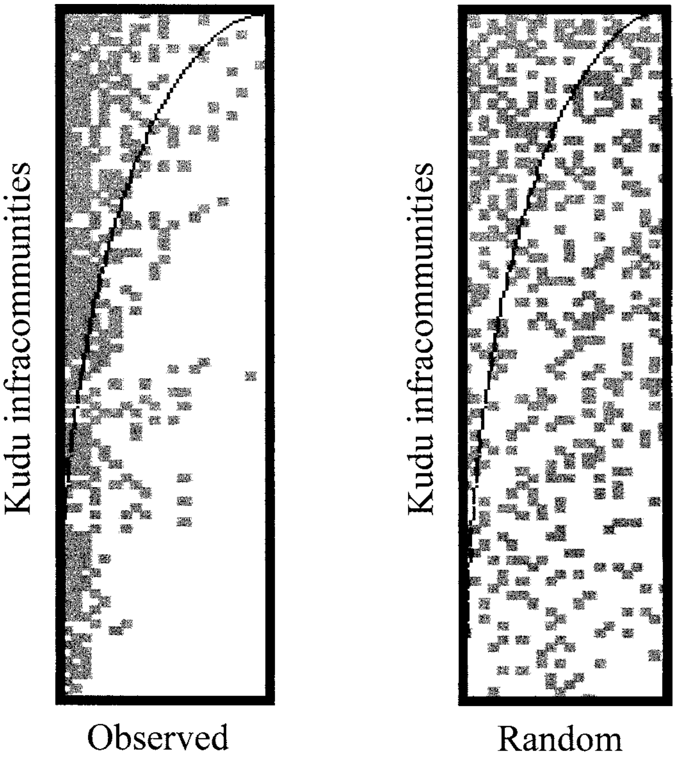

FIGURE 3. Maximally packed presence–absence matrices for observed kudu infracommunities from the Kruger National Park and 1 randomly generated community based on observed data.

Fisher and Lindemayer (2002) have recently warned that blindly relying on *P*-values generated by null models in general and the nestedness temperature calculator in particular may lead to false conclusions. Their point is well taken and has been foreshadowed for several decades as the heart of 1 of the longest debates in community ecology (Lewin, 1983; Gotelli, 2000). Statistical significance acquired from null models does not necessarily equate with ecological significance and should not be used without a thorough understanding of the biology of a given system and the assumptions and limitations of the model. However, null models, like inferential statistics, are powerful tools, which can be used to gain insight that would be otherwise unavailable. Fisher and Lindemayer (2002) demonstrated that the nestedness temperature calculator may be susceptible to type I error with some data sets and thus may not be appropriate for communities composed primarily of ubiquitous and rare species or where statistical significance approaches the desired α-level. Despite the limitations of the nestedness temperature calculator, Fisher and Lindemayer (2002) acknowledge its usefulness as an analytical tool.

On the basis of this analysis, it can be concluded that the helminth parasites of the greater kudu from southern Africa show significant levels of association with hosts of a different geographic location and demography. As a result, parasite communities from these various groups can readily be distinguished from each other and lend a level of predictability to community patterns. Null model analyses displayed high levels of nonrandomness among infracommunities of KNP and suggest a higher-level order that can be attributed to both the accumulation of species over time and the segregation of species among different age-class hosts.

TABLE VIII. Species co-occurrence summary for all helminths and enteric nematodes from Kruger and Etosha National Parks (C-obs = observed C-score value, C-sim = average C-score from randomized communities).

	All worms present			Enteric nematodes		
	C-obs	C-sim	*P* value	C-obs	C-sim	*P* value
KNP						
All kudus	92.1	83.6	0*	109.6	89.5	0*
Adults and juveniles	28.35	28.22	0.39	25.68	24.6	0.15
Calves	8.9	8.7	0.28	11.29	11.1	0.23
ENP						
Adults	28.35	28.22	0.39	6.04	6.33	0.9

* None of the C-score values from the 5,000 randomized communities was greater than the observed C-score value.

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J. Parasitol., 92(6), 2006, pp. 1180–1190

AN EXAMINATION OF THE INFRACOMMUNITIES AND COMPONENT COMMUNITIES FROM IMPALA (*AEPYCEROS MELAMPUS*) IN THE KRUGER NATIONAL PARK, SOUTH AFRICA

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ABSTRACT: The intestinal helminth parasites of the impala from the Kruger National Park, South Africa, were examined to describe the parasite community structure. Demographic variation and the associated differences in behavior were used to further investigate the patterns of community composition. Monte Carlo simulations were performed to test for differences in species richness and mean abundance between the various demographic groups, and nonmetric multidimensional scaling ordination was used to compare community composition. Seventeen species of nematodes, totaling more than 1.3 million worms, were recovered. Males harbored a greater number of nematode species than did females, but adult females were more heavily infected than their male counterparts. Lambs acquired infections early in life, and their parasite community composition rapidly approached that of the older animals. The parasite community in the juvenile and adult males was significantly different from the community of the adult females. These data suggest that social and feeding behavior of the different age–sex classes structure the parasite component community of impala. Additionally, the distinction between common and rare parasites, and their classification in other herbivores, implies complex transmission dynamics that includes extensive species sharing within the Kruger National Park.

Recently, Fellis et al. (2003) examined the infracommunities of the greater kudu (*Tragelaphus strepsiceros*) from 2 locations in southern Africa. In this case, host demographics were found to be a reliable predictor of parasite infracommunity structure. Specifically, behavioral changes associated with aging appear to alter the degree of exposure to infective larvae of numerous nematode species. Additionally, the component parasite community structure was more similar for kudu within a given location than between locations. Environmental differences are likely the dominant factor in producing the observed differences, but presence or absence of other hosts can not be ignored (Fellis et al., 2003).

A survey from 1980 through 1982 produced a large data set for the nematode infracommunities of impala (*Aepyceros melampus*) in the Kruger National Park, South Africa. The present study extends the knowledge of parasite communities in Kruger National Park by describing the nematode component community of this antelope species. Based on the infracommunity study of kudu by Fellis et al. (2003), we predict that host demographics will affect the infracommunities in impala. The component community is also compared to those of other large herbivores residing in the Kruger National Park, and a discussion of ideas pertaining to species sharing is presented.

METHODS

Study site

The Kruger National Park (KNP) is in the northeast portion of South Africa. It is a 19,548-km^2 park and experiences a seasonal climate, from warm or hot summers, to mild winters. Annual rainfall in the KNP averages 600–700 mm. Impala were collected from the southern portion of the park where few areas are >5 km from a water source (Redfern et al., 2003). Vegetation in the southern region is fairly diverse, with 4 veld types being recognized (Boomker et al., 1989).

Study animals

The impala is a medium-sized bovid belonging to the tribe Aepycerotini. Males are larger (60 kg) than females (45 kg) and possess rigid, S-curved horns. They are intermediate feeders, capable of eating browse, but preferentially consuming grass when it is green and available (Okello et al., 2002; Wronski, 2002). Impala are gregarious and territorial (Estes, 1990). Females congregate in discrete clans. During the lambing season, pregnant females isolate in cover several hours before birth. Lambs typically associate with each other, only returning to their mother to nurse, during herd movements, and for protection. Male offspring leave the natal clan when they develop obvious male traits and form temporary peer groups, whereas females usually remain in the maternal herd.

Adult male impala associate in bachelor herds that adhere to a linear hierarchy. Top males compete for territory during the rut, which commences in mid-April and persists through July and mid-August. The male maintains 1 or 2 lookout points where he also defecates. During this time, territorial males will remain alone or as the only male in a female herd. Although the male remains in a small territory, probably not even a hectare in size, he is physically exhausted and emaciated from herding his harem and keeping other males away. He then rejoins the bachelor herd at the bottom of the hierarchy ladder at the end of the breeding season.

Data collection

Beginning in January 1980 and ending in December 1982, 158 impala were culled from the southern region of KNP. A concerted effort was made to take 1 impala of each age class (adult, juvenile, lamb) on a monthly basis. Once killed, the animals were assigned an age class (adult, juvenile, or lamb) and sex (male or female). At necropsy, enteric parasites were identified and counted for each individual impala, following the procedures of Boomker et al. (1989). Reference specimens are deposited into the National Collection of Animal Helminths at the Onderstepoort Veterinary Institute.

Received 5 May 2006; revised 20 September 2006; accepted 26 October 2006.

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Age classification follows Hanks and Howell (1975). Lambs are defined as individuals <6 mo of age. Female impala older than 6 mo are difficult to distinguish, so juvenile females were classified as adults (ADF). By the end of the first year, males leave the natal herd and are considered juveniles (JUM). They retain juvenile status until their fourth year, when they become adults (ADM) and can acquire territory.

Data analysis

Descriptive analysis of the parasite community consisted of investigations into differences in average intensity and helminth richness between the various classifications of impala. Unless specifically stated in the results, only those nematodes identified to species were included in the analyses. This eliminated larval and female worms. Investigations into seasonal changes of the infracommunity of adult impala were attempted, but monthly sample sizes for each age–sex class rarely exceeded 5 individuals, with a few months consisting of 1 or 2 individuals. Consequently, data were pooled across month. In nearly all cases, the data did not meet the requirements for parametric statistics, most notably the requirement for equal variances. Natural log transformations were, therefore, performed on worm burden data and, if the assumptions for parametric statistics were achieved, the appropriate parametric test was performed to investigate differences in the means. If transformation of the data did not correct for heterogeneity of variances, the nonparametric equivalents to standard parametric tests were utilized to determine statistical significance. When significant differences were observed, a Steel-type multiple comparison (MC) post-hoc test was performed to look at differences among treatment levels.

Analyses also extended beyond standard statistical methods. Age–sex classes represent a composite between age and sex effects. Distinguishing between these 2 components using parametric statistics is difficult in that unequal sample sizes, distributions, and variances can limit statistical power. As such, randomization tests were performed (Manly, 1991; Crowley, 1992). To test for a sex effect, the sex variable was randomized among the adult impala for 10,000 iterations, maintaining the observed proportion of male to female adults. This kept overall prevalence and intensity for each nematode species equal throughout the simulations. Furthermore, richness and mean worm burden for each impala remained constant, even though age and sex categories changed. For each iteration, a test value for species richness and worm burden was obtained by taking the absolute value of the difference between the ADF and ADM values. The P value is the number of iterations that produced an absolute difference that is equal to or greater than the difference observed in the unaltered data set divided by the number of iterations (Manly, 1991). For these simulations, a P value of ≤ 0.05 was considered significant. Age differences between the ADM and JUM were also examined using the same methods described previously. The age variable for the males, excluding lambs, was randomized instead of the sex variable.

Randomization tests were also performed to investigate infracommunity differences between the various age–sex classes. Unlike previous procedures, we randomized the data for each nematode species to remove correlations in host occupancy, i.e., the data for each species are randomized independently for the remaining species. Overall prevalence is kept constant, and only the distribution among the impala is changed. Differences in richness and worm burden between the various age–sex categories were inspected.

Infracommunity similarity between individual impala was examined with ordination. Nonmetric multidimensional scaling (NMDS) uses quantitative data on species in multiple hosts to construct a dissimilarity matrix. From this matrix, the rank order dissimilarities are used to construct an ordination plot so that rank order distances of each host are as similar to the dissimilarity matrix as possible. NMDS has advantages over other ordination procedures that make it more suitable for a study such as this. Thus, there are no requirements regarding the distribution of the underlying data, and both presence or absence and abundance of each helminth species can be used to determine dissimilarity values (McCune and Mefford, 1999). NMDS of the presence/absence data produced a 1-dimensional ordination (distance = Sorensen, stress = 0.19) that reflects the variation in species richness among individual impala (McCune and Mefford, 1999). So, the analysis was rerun using Sorensen distances of abundance data. Sorensen distances are suitable for both abundance and presence/absence data, and were used for a similar analysis in the greater kudu (Fellis et al., 2003).

Differences in community composition between the various methods of classification of the impala can be tested with an analysis of similarities (ANOSIM) and indicator species analysis. ANOSIM is an analog of ANOVA, comparing compositional dissimilarity (Sorensen distances) within each group to those between the various groups (Clarke, 1993). In this data set, ANOSIM was performed on impala that were classified by age, sex, and age–sex. Indicator species analysis utilizes both prevalence and abundance data to calculate an indicator value (IV) for each nematode species. Monte Carlo analysis (10,000 iterations) was used to determine if the largest IV for each species occurs more often than dictated by chance alone (McCune and Mefford, 1999). Furthermore, the IV is a measure of the percentage of perfect indication, i.e., how often that particular species can correctly assign a classification to an unknown impala. NMDS and indicator species analysis were performed on PC-ORD software (McCune and Mefford, 1999); the vegan package in R 2.2.1 (http://www.R-project.org) was used for ANOSIM.

RESULTS

Seventeen species of nematodes, totaling >1.3 million worms, were recovered from the gastrointestinal tracts of impala (Table I). Following the classification of Fellis et al. (2003), 10 species are common (>50% prevalence), 2 are intermediate (between 10% and 50% prevalence), and 5 are rare (<10% prevalence). All but 2 species belong to the Trichostrongylidae. *Oesophagostomum columbianum* and *Strongyloides papillosus* are both strongylids. Infection by all but 1 species occurs via ingestion of L3 worms. The exception was *S. papillosus*, whose routes of infection are percutaneous and transmammary (Lyons et al., 1970).

Community richness and average worm load are summarized in Table II. Total nematode species richness differs between age (KW: $P < 0.001$) and sex (KW: $P < 0.005$) and between sexes within an age class (KW: $P < 0.0001$). However, natural log-

TABLE I. Percent prevalence, mean abundance (±SE), and mean intensity (±SE) for gastrointestinal nematodes recovered from 158 impala of Kruger National Park, South Africa.

Species	Prevalence	Abundance	Intensity
*Cooperia conochaeti**	4.4	6.7 ± 5.1	150.9 ± 109.2
*Cooperia fuelleborni**	17.1	59.0 ± 18.3	345.1 ± 89.3
*Cooperia hungi**	89.2	1086.8 ± 161.3	1217.9 ± 177.7
*Cooperia neitzi**	2.5	1.3 ± 0.7	50.3 ± 10.2
*Cooperioides hamiltoni**	94.9	869.5 ± 146.6	915.9 ± 153.6
*Cooperioides hepaticae**	81.0	147.6 ± 29.4	182.2 ± 35.7
*Haemonchus bedfordi**	3.8	1.9 ± 0.9	50.5 ± 14.1
*Haemonchus contortus**	0.6	0.01 ± 0.01	2.0 ± 0.0§
*Haemonchus krugeri**	64.6	246.8 ± 54.1	382.3 ± 80.9
*Haemonchus vegliai**	2.5	0.5 ± 0.48	20.5 ± 18.2
*Impalaia tuberculata**	81.6	745.6 ± 114.0	913.2 ± 135.4
*Longistrongylus sabie**	82.3	174.9 ± 25.4	212.5 ± 29.9
Oesophagostomum columbianum†	75.9	84.1 ± 13.2	110.7 ± 16.7
Strongyloides papillosus‡	88.6	325.6 ± 22.8	367.4 ± 23.5
*Trichostrongylus deflexus**	89.9	1688.2 ± 253.8	1878.4 ± 278.0
*Trichostrongylus falculatus**	22.8	19.9 ± 4.5	87.6 ± 15.1
*Trichostrongylus thomasi**	85.4	375.4 ± 42.5	439.4 ± 47.6

* Trichostrongylidae; infection via consumption.
† Strongylidae; infection via consumption.
‡ Strongyloididae; vertical infection and via percutaneous transmission.
§ One individual was infected.

transformed mean intensities differ only between age (KW: $P < 0.0001$) and age–sex (KW: $P < 0.001$). In general, male impala harbor a greater richness of intestinal nematodes than do females. In fact, the 5 rare species are unique to males (Table III). Within the different age classes, juvenile impala harbor the greatest number of nematode species, and lambs have the lowest mean worm burden (Table II). Female lambs typically possess fewer species and total worms than do older impala (Table II). ADF, although infected with approximately the same number of nematode species, tend to possess a larger worm burden than both ADM and JUM.

Randomization tests examining the effect of sex on the infracommunity of ADM and ADF revealed that average species richness did not differ ($P > 0.05$), but mean intensity was significantly different ($P < 0.042$). This agrees with the post-hoc MC performed on the data, and strongly suggests that adult worm burden is affected by the sex of the host. Age differences between the male impala, excluding lambs, was found to be a significant contributor to species richness ($P < 0.02$), but not to worm burden ($P > 0.05$). This confirms the result of the Steel-type multiple comparison test (Munzel and Hothorn, 2001) for both log-transformed intensity ($P > 0.05$) and species richness ($P < 0.022$).

A 2-dimensional NMDS ordination of abundance data explains 82.7% of the variation (stress = 0.14) among the infracommunities of impala (Fig. 1). Two points are clear. First, the

TABLE II. Infection summary of the impala collected from Kruger National Park. Summaries included all impala, and impala classified by sex, age, and age-sex. Differences in species richness (±SE) and natural-log-transformed intensity (Ln ± SE) within the individual classifications were tested for normality, and the appropriate statistical test was performed. When a significant *P* value was obtained, a Steel-type multiple comparison test was performed. Values with the same superscript are considered not significantly different. N = total number of individuals, S = species richness, N.S. = not significant.

Classification	N	S	Test (*P* value)	Ln (intensity)	Test (*P* value)
Total	158	8.87 ± 0.18		8.09 ± 0.09	
Sex					
Male	108	9.30 ± 0.17	Kruskal-Wallis	8.10 ± 0.08	N.S.
Female	50	7.96 ± 0.40	(<0.005)	8.08 ± 0.24	
Age					
Adult	98	8.77 ± 0.21*	Kruskal-Wallis	8.28 ± 0.11*	Kruskal-Wallis
Juvenile	45	9.73 ± 0.19†	(<0.001)	8.20 ± 0.17*	(<0.0001)
Lamb	15	7.00 ± 0.94*		6.59 ± 0.34†	
Age-sex					
Adult male	56	8.91 ± 0.27*	Kruskal-Wallis	8.08 ± 0.11*	Kruskal-Wallis
Adult female	42	8.57 ± 0.35*	(<0.0001)	8.54 ± 0.22*	(<0.001)
Juvenile male	45	9.73 ± 0.19*		8.20 ± 0.12*	
Lamb male	7	9.57 ± 0.53*†		7.62 ± 0.19*	
Lamb female	8	4.75 ± 1.24†		5.68 ± 0.41†	

TABLE III. Percentage of prevalence and mean intensity (±SE) for the 108 male and 50 female impala.

	Prevalence		Intensity	
Species	Male	Female	Male	Female
Cooperia conochaeti	6.5	0	150.9 ± 27.8	0*
Cooperia fuelleborni	16.7	18.0	342.3 ± 39.0	350.9 ± 83.8
Cooperia hungi	91.7	84.0	888.2 ± 67.6	1994.9 ± 512.5
Cooperia neitzi	3.7	0	50.3 ± 2.0	0*
Cooperioides hamiltoni	98.1	88.0	554.0 ± 52.1	1787.5 ± 457.0
Cooperioides hepaticae	86.1	70.0	169.8 ± 22.6	215.0 ± 95.7
Haemonchus bedfordi	5.6	0	50.5 ± 3.3	0*
Haemonchus contortus	0.9	0	2.0 ± 0†	0*
Haemonchus krugeri	66.7	60.0	263.2 ± 47.7	668.2 ± 179.1
Haemonchus vegliai	3.7	0	20.5 ± 3.5	0*
Impalaia tuberculata	86.1	72.0	533.8 ± 61.0	1893.4 ± 352.7
Longistrongylus sabie	86.1	74.0	149.7 ± 13.3	370.6 ± 81.5
Oesophagostomum columbianum	82.4	62.0	102.4 ± 16.7	134.5 ± 29.3
Strongyloides papillosus	92.6	80.0	387.8 ± 28.3	316.5 ± 32.5
Trichostrongylus deflexus	92.6	84.0	1379.5 ± 187.3	3066.4 ± 728.5
Trichostrongylus falculatus	19.4	30.0	65.2 ± 3.8	118.9 ± 18.2
Trichostrongylus thomasi	90.7	74.0	325.2 ± 34.0	741.7 ± 116.1

* None of the impala harbored the nematode.

female lambs form a group separate from the older impala. The 4 most distant female lambs in ordination space are those individuals collected in January and less than 1 mo of age. The February collection consisted of 2 female lambs, and these individuals are more similar to the older impala (=closer in ordination space) than are the youngest lambs. NMDS ordination also reveals 2 groups, an ADM/JUM group and an ADF group. The pattern or groups signified by NMDS was further tested using ANOSIM. Second, significant differences were observed between the age ($P = 0.008$), sex ($P < 0.001$), and age–sex groupings ($P < 0.0001$). When testing differences in age–sex, only the comparison between ADM and JUM was not significant (ANOSIM: $P > 0.05$).

Indicator species analysis was performed to determine if certain nematode species are more indicative of a particular age and/or sex classification (Table IV). Like NMDS and ANOSIM, indicator values include both the presence/absence and abundance data within and between the different classification schemes. When examining age, 7 nematodes produce significant indicator values, and 6 of these are the common species; only *O. columbianum* and *Cooperioides hepaticae* are indicative of an age group other than adult. Only 3 nematodes with significant indicator values for age also predict sex. Along with *S. papillosus*, these nematodes are common in the impala, but *Trichostrongylus falculatus* occurs just occasionally. All but one, *S. papillosus*, most accurately predict that the impala host is female. Analysis by age–sex classification produces 6 significant indicator values. Nearly all are common species and are indicative of ADF. *Haemonchus vegliai* is a rare species and is most indicative of male lambs.

DISCUSSION

Dogiel et al. (1964) identified similarities in the intestinal component communities of animals with overlapping diets, a pattern that has been identified numerous times in fishes (Price and Clancy, 1983; Bell and Burt, 1991; Nelson and Dick, 2002; Johnson et al., 2004). Since most of the helminths in the intestine are acquired via ingestion of infective stages, diet of the host should play a major role in structuring the component community. In the present study, infection occurs via forage consumption for nearly all of the nematodes recovered from the impala. The single exception, *S. papillosus*, is transmitted percutaneously, or via suckling. Vertical transmission is the probable route of infection for lambs, since all individuals >2 wk old were infected. Successful transmission for the remaining nematode species requires that the infective larvae to disperse onto, and up, vegetation so that they can be consumed. Vertical dispersal is dependent on several factors, including the plant species (Callinan and Westcott, 1986; Niezen et al., 1998). Grazers are more likely to consume the infective larvae because their food source is closer to the ground, and larvae are required to only travel a short distance up a blade of grass. On the other hand, browsers consume fallen leaves, foliage, and other woody plant parts. Fallen leaves provide a means by which parasitic nematodes can infect the browsing host. When the host is consuming dicots, then infective larvae must disperse a considerable distance up the stem and onto the leaves to ensure transmission. Reports on lateral and vertical dispersal of L3 worms suggest that most remain within 15 cm of the dung pat (Callinan and Westcott, 1986; Stromberg, 1997). Rainfall can increase the dispersal distance (Stromberg, 1997), however, and dew likely aids in dispersal up blades of grass (Gruner et al., 1989). Intermediate feeders, such as the impala, are exposed to nematode species commonly found in both grazers and browsers. Thus, their nematode fauna will include species common to both grazers and browsers, and the infracommunity composition will reflect sex and age-class variation in feeding behavior.

The nematode infracommunity of impala also reflects the demographics of the host. This was seen in the ordination of abundance data, where the lambs formed a group separate from the juvenile and adult group as a whole (Fig. 1). An obvious factor that could produce these unique communities is age of the host.

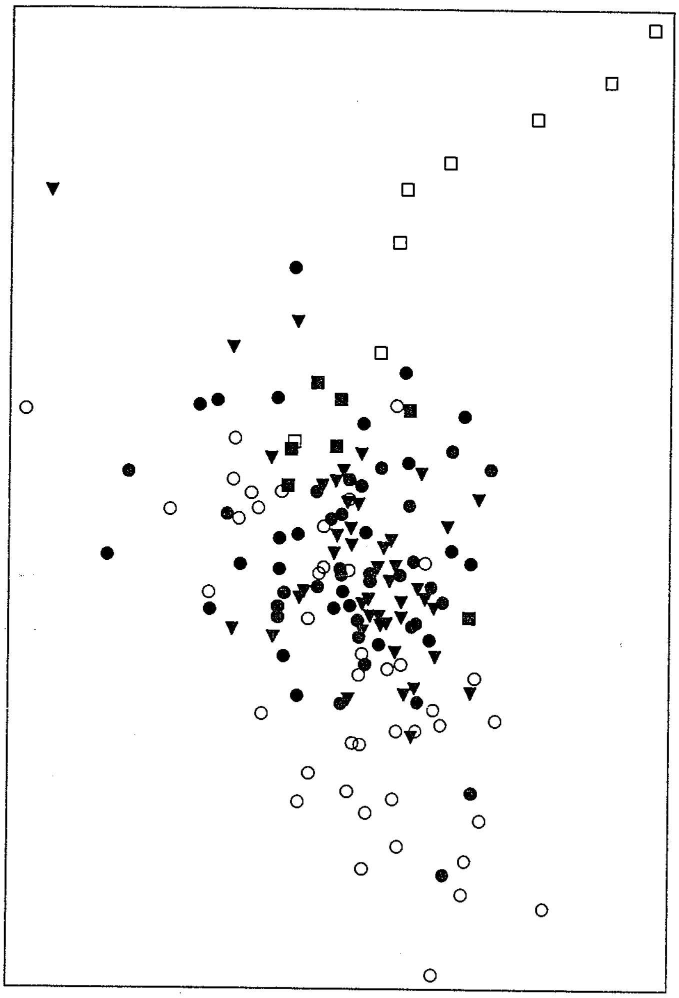

FIGURE 1. Nonmetric multidimensional scaling solution for the infracommunities of 158 impala using abundance data (axis 1 = 29.5%, axis 2 = 52.2%, stress = 0.14). Only those nematodes that were identified to the species level were included in the analysis. (● = Adult male, ○ = adult female, ▼ = juvenile male, ■ = lamb male, □ = lamb female.)

Aging increases the time of exposure to the infective stages, and thus the likelihood of infection. To illustrate, the youngest impala were CAF. Two impala <2 wk of age were uninfected or infected with larval stages of a single species. By 1 mo, CAF were infected with an average of 2 different species. Although the lambs are nursing until 5 mo of age, they are naive and consume a wide variety of vegetation (Frost, 1981). Therefore, impala lambs rapidly acquire additional nematode species, and their infracommunities begin to resemble those of the older impala. The oldest lambs in the study were 6 mo old. Their nematode species richness was equal to the average across all impala, but their mean worm burden was much lower than the average for the older individuals. Nursing reduces the nutritional requirement and hence the food intake of the lambs, resulting in a lower mean intensity for this age group.

The age effect is further compounded by changes in social behavior. Animals that share diets and habitats are often exposed to the same parasites (Dogiel et al., 1964; Holmes and Podesta, 1968; Price and Clancy, 1983). For example, the CAF, by remaining in the natal herd, harbor an infracommunity that resembles the ADF. All of the nematode species recovered from the CAF were also recovered from the ADF, albeit in lower numbers (Tables V,VI). Males, however, leave the herd by the first year and form juvenile clans. These juveniles remain at the periphery of the female herd; thus, they are exposed to the same infective stages as the females in addition to those stages not present in the female clan's feeding area. Increased movement of JUM exposes these individuals to a greater variety of infective stages, most notably those of species that utilize other ungulates as their primary host. Later in life, the rare species acquired by young males are usually lost and seldom replaced.

Infracommunity differences are caused by the presence and abundance of specific species. Only 2 species are most indicative of juveniles (Table IV). *Oesophagostomum columbianum* infects over 86% of the JUM, compared to 71% of adults and 73% of lambs. The higher prevalence in JUM is likely because of increased movement rates of the juvenile males when they leave the natal herd. Those individuals that are not infected with *O. columbianum* are able to acquire the infective stage released by other susceptible ungulates residing in the same area, while infected individuals retain their infection. There is a slightly different explanation for the second nematode. *Cooperioides*

TABLE IV. Indicator values (IV) and *P* value of those nematode species that most accurately predict impala by age, sex, and age-sex. I.C. = indicative class, A = adult, J = juvenile, F = female, M = male, ADF = adult female, CAM = lamb male, N.S. = not significant.

	Age			Sex			Age-sex		
Species	IV	I.C.	*P*	IV	I.C.	*P*	IV	I.C.	*P*
Cooperioides hamiltoni	62.5	A	0.007	65.4	F	0.024	55.8	ADF	0.011
Impalaia tuberculata	65.7	A	0.001	71.5	F	0.001	61.9	ADF	0.001
Longistrongylus sabie	62.6	A	0.001	64.7	F	0.005	56.1	ADF	0.001
Oesophagostomum columbianum	51.9	J	0.004		N.S.			N.S.	
Trichostrongylus thomasi	55.8	A	0.002		N.S.		42.4	ADF	0.008
Cooperioides hepaticae	56.1	J	0.019		N.S.			N.S.	
Cooperia hungi	50.4	A	0.048		N.S.			N.S.	
Strongyloides papillosus		N.S.		54.3	M	0.017		N.S.	
Trichostrongylus falculatus		N.S.		22.1	F	0.030		N.S.	
Haemonchus vegliai		N.S.			N.S.		14.1	CAM	0.024
Trichostrongylus deflexus		N.S.			N.S.		44.3	ADF	0.036

TABLE V. Percentage of prevalence of each nematode species in the various age-sex classes of impala. The number of impala in each category is listed in parentheses. ADM = adult male, ADF = adult female, JUM = juvenile male, CAM = lamb male, CAF = lamb female.

	% Prevalence				
Species	ADM (n = 56)	ADF (n = 42)	JUM (n = 45)	CAM (n = 7)	CAF (n = 8)
Cooperia conochaeti	7.1	0	6.7	0	0
Cooperia fuelleborni	17.9	19.0	13.3	28.6	12.5
Cooperia hungi	89.3	90.5	93.3	100.0	50.0
Cooperia neitzi	5.4	0	2.2	0	0
Cooperioides hamiltoni	98.2	97.6	100.0	85.7	37.5
Cooperioides hepaticae	75.0	71.4	97.8	100.0	62.5
Haemonchus bedfordi	3.6	0	6.7	14.3	0
Haemonchus contortus	0	0	2.2	0	0
Haemonchus krugeri	62.5	61.9	71.1	71.4	50.0
Haemonchus vegliai	1.8	0	4.4	14.3	0
Impalaia tuberculata	82.1	78.6	91.1	85.7	37.5
Longistrongylus sabie	83.9	83.3	88.9	85.7	25.0
Oesophagostomum columbianum	76.8	64.3	86.7	100.0	50.0
Strongyloides papillosus	92.9	76.2	91.1	100.0	100.0
Trichostrongylus deflexus	85.7	92.9	100.0	100.0	37.5
Trichostrongylus falculatus	17.9	33.3	24.4	0	12.5
Trichostrongylus thomasi	91.1	88.1	93.3	71.4	0

hepaticae is acquired early in life (Pletcher et al., 1988). The adult worms live in the bile duct and stimulate formation of hepatic lesions (Pletcher et al., 1988; Anderson, 1992). Pletcher et al. (1988) recorded the heaviest infections from the yearlings, or JUM, and prevalence and mean intensity declined as the impala aged. They concluded that the decrease in prevalence and intensity of *C. hepaticae* is a result of acquired, or protective, immunity, which is consistent with the decrease in prevalence and intensity observed when comparing JUM to ADM. Mean intensity of *C. hepaticae* in ADF is slightly larger than JUM. However, controlling for outliers with a log transformation reveals that JUM are in fact more heavily infected than the ADF (ANOVA: $P < 0.0003$). The most severe infections are likely occurring in the yearling females, which are classified as adults and skew the mean intensity in ADF.

The remaining species that are most indicative of adults (Table IV) reflect typical aging effects. Specifically, the mean intensity of each species increases for each age group (Table VII). Prevalence increases as the lambs become juveniles and decreases slightly as they become adults. Studies have shown that domestic sheep and cattle are able to develop an immune response to a number of nematode species, including *Cooperia*

TABLE VI. Mean intensity (±SE) of each nematode species for the various age-sex classes of impala. The number in parentheses indicates how many individual impala were included in the sample. ADM = adult male, ADF = adult female, JUM = juvenile male, CAM = lamb male, CAF = lamb female.

	Mean intensity				
Species	ADM (n = 56)	ADF (n = 42)	JUM (n = 45)	CAM (n = 7)	CAF (n = 8)
Cooperia conochaeti	221.5 ± 51.6	0*	56.7 ± 8.8	0*	0*
Cooperia fuelleborni	407.5 ± 66.3	388.5 ± 96.0	301.8 ± 43.4	137.5 ± 46.8	50.0 ± 0†
Cooperia hungi	958.2 ± 92.2	2187.8 ± 580.4	893.3 ± 111.1	357.9 ± 57.4	162.5 ± 68.7
Cooperia neitzi	50.3 ± 3.3	0*	50.0 ± 0†	0*	0*
Cooperioides hamiltoni	612.0 ± 87.0	1913.5 ± 511.4	517.0 ± 58.2	300.0 ± 123.9	66.7 ± 5.1
Cooperioides hepaticae	102.9 ± 29.1	247.7 ± 112.2	243.3 ± 36.8	109.3 ± 36.7	19.0 ± 7.2
Haemonchus bedfordi	14.0 ± 2.1	0*	75.0 ± 3.7	50.0 ± 0†	0*
Haemonchus contortus	0*	0*	2.0 ± 0†	0*	0*
Haemonchus krugeri	405.9 ± 90.6	760.3 ± 206.6	129.4 ± 17.1	120.0 ± 23.5	69.5 ± 31.5
Haemonchus vegliai	3.0 ± 0†	0*	2.0 ± 0.0	75.0 ± 0†	0*
Impalaia tuberculata	624.8 ± 103.3	2056.5 ± 392.6	472.9 ± 70.3	251.7 ± 57.2	100.0 ± 38.5
Longistrongylus sabie	156.5 ± 21.1	389.8 ± 90.5	157.0 ± 17.4	46.7 ± 11.3	35.0 ± 12.5
Oesophagostomum columbianum	99.5 ± 29.8	151.7 ± 33.5	116.7 ± 17.7	41.3 ± 11.4	19.0 ± 9.4
Strongyloides papillosus	339.7 ± 37.0	346.9 ± 37.5	430.2 ± 47.1	496.4 ± 96.4	195.0 ± 36.5
Trichostrongylus deflexus	1382.7 ± 314.0	3286.7 ± 815.5	1499.7 ± 227.8	585.3 ± 432.8	201.7 ± 47.8
Trichostrongylus falculatus	74.5 ± 5.4	119.9 ± 20.6	56.7 ± 5.7	0*	105.0 ± 0†
Trichostrongylus thomasi	392.1 ± 57.9	741.7 ± 126.7	266.3 ± 33.2	138.6 ± 64.5	0*

* None of the impala harbored the nematode.
† A single impala was infected.

TABLE VII. Percentage of prevalence and mean intensity (±SE) for 108 adult, 45 juvenile, and 15 lamb impala. A = adult, J = juvenile, C = lamb.

Species	Prevalence			Mean intensity		
	A	J	C	A	J	C
Cooperia conochaeti	4.1	6.7	0.0	221.5 ± 193.0	56.7 ± 34.2	0*
Cooperia fuelleborni	18.4	13.3	20.0	399.1 ± 126.9	301.8 ± 118.8	108.3 ± 58.3
Cooperia hungi	89.8	93.3	73.3	1489.2 ± 275.1	893.3 ± 115.0	286.8 ± 56.3
Cooperia neitzi	3.1	2.2	0.0	50.3 ± 14.4	50.0 ± 0.0	0*
Cooperioides hamiltoni	98.0	100.0	60.0	1167.8 ± 234.6	517.0 ± 58.2	222.2 ± 94.8
Cooperioides hepaticae	73.5	97.8	80.0	163.2 ± 58.8	243.3 ± 37.2	71.7 ± 24.9
Haemonchus bedfordi	2.0	6.7	6.7	14.0 ± 11.0	75.0 ± 14.4	50.0 ± 0†
Haemonchus contortus	0.0	2.2	0.0	0*	2.0 ± 0†	0*
Haemonchus krugeri	62.2	71.1	60.0	557.0 ± 130.5	129.4 ± 20.2	97.6 ± 25.0
Haemonchus vegliai	1.0	4.4	6.7	3.0 ± 0†	2.0 ± 0.0	75.0 ± 0†
Impalaia tuberculata	80.6	91.1	60.0	1222.8 ± 210.6	472.9 ± 73.6	201.1 ± 50.6
Longistrongylus sabie	83.7	88.9	53.3	256.1 ± 45.8	157.0 ± 18.5	43.8 ± 10.3
Oesophagostomum columbianum	71.4	86.7	73.3	119.6 ± 26.3	116.7 ± 19.0	33.2 ± 9.0
Strongyloides papillosus	85.7	91.1	100.0	342.4 ± 28.7	430.2 ± 49.4	335.7 ± 61.9
Trichostrongylus deflexus	88.8	100.0	66.7	2236.2 ± 432.4	1499.7 ± 227.8	470.2 ± 302.1
Trichostrongylus falculatus	24.5	24.4	6.7	101.0 ± 21.6	56.7 ± 11.6	105.0 ± 0†
Trichostrongylus thomasi	89.8	93.3	33.3	539.1 ± 68.8	266.3 ± 34.4	138.6 ± 76.3

* None of the impala harbored the nematode.
† A single impala was infected.

spp., *Haemonchus* spp., and *Trichostrongylus* spp. (Armour, 1989; Ploeger et al., 1995; Vercruysse and Claerebout, 1997). In each study, prevalence or intensity, or both, decreased as the animal aged. Of the species examined in the previous studies, only *Haemonchus contortus* was recovered from the impala. A single impala harbored this nematode, which implies an accidental infection and not host immunity. It is unlikely that the *Cooperia* spp., *Haemonchus* spp., and *Trichostrongylus* spp. occurring in the impala are stimulating a significant immunological memory response, because mean intensity increases with age of the host.

Age is not the only factor associated with infracommunity differences. Sex of the individual animal influences their feeding preference and social behavior. In the impala, 5 nematode species are indicative of a specific sex (Table IV). All but one, *S. papillosus*, predict the sex of the host to be female. The species most indicative of females are those most likely to benefit from the reinfection that occurs within the female clans (Altizer et al., 2003). Reinfection increases the mean intensity among the females of the group, and improves the chances that the uninfected members of the group are acquiring the infection. Males gain reprieve from reinfection because their clans are smaller (Estes, 1990), and they tend to move more than the female herds (Murray, 1982).

Increased home range and rates of movement more likely expose males to a greater variety of nematode species. In the Sengwa Wildlife Research Area, Zimbabwe, the average annual home range of 4-yr-old males is 90 ha, and declines to 49 ha in males 5–6 yr of age (Murray, 1982). Furthermore, JUM travel an average of 1.2 km after leaving their natal herd (Murray, 1982). These estimates also apply to impala of KNP. Dispersal and large home ranges explain why the JUM harbor all of the nematode species that infect impala in KNP (Table V). Moreover, adults >4 yr of age avoid the rare infections by restricting the range they travel during any given year.

Female impala congregate in large herds and have an average home range of 51.6 ha (Murray, 1982). The natal clans typically remain in a small area, but they will move during the dry season as food resources dwindle. Members of the female herds can only be exposed to those infective stages present in the area where they reside. Therefore, female clans are not exposed to the rare species that infect the males. However, less movement increases the chance of repeated exposure to infective stages in their home range (Altizer et al., 2003). The most extreme example of reinfection occurred during the drought of 1982. J. Boomker (unpubl. obs.) found that impala at Skukuza congregated on a golf course, which was maintained with regular watering and careful tending. This soon resembled an irrigated pasture with the numbers of worms in individual animals trebling and ultimately causing the death of the antelope. In other vertebrates, studies have demonstrated an increase in parasite prevalence and intensity within larger groups of individuals (Freeland, 1979; Brown and Brown, 1986; Moore et al., 1988; Davies et al., 1991; Altizer et al., 2003). The relationship likely results from an increased risk of infection, especially if a few members currently harbor infections. Impala exhibit this trend, with members of the larger ADF clan having greater worm burdens than their male counterparts.

Food selection and variation in dispersal of the infective larvae are factors affecting the community composition differences between adult male and female impala. During the rut, the strongest males claim the prime territory, which contain most of the grass and shrubs consumed by the females. At this time, the territorial males constantly attempt to exclude other males while keeping the females within their territory (Van Rooyen and Skinner, 1989). These males have less time for feeding, and must consume what is available without being selective. Typically, the males will consume significantly fewer dicots than are consumed by bachelor males on the periphery of their territory (Van Rooyen and Skinner, 1989). Females, in contrast, are very selective, preferentially consuming the high-quality dicots (Rodgers, 1976; Fritz and De Garine-Wichatitsky, 1996) within the male impala's territory (Van Rooyen and Skinner, 1989). The difference in food preference produces differential exposure probability to the various infective stages present in the habitat. Thus, indiscriminate feeders, i.e., territorial males, are more likely to consume and become infected with those species commonly occurring in other antelope and ungulate species. This assumes that vegetation type is affecting the dispersal of infective larvae, which has been demonstrated for a variety of common pasture plants (Callinan and Westcott, 1986; Niezen et al., 1998; Hoste et al., 2006). Alternatively, preferential food selection may be providing a type of antihelminthic treatment against certain nematode species, particularly *Haemonchus* spp. Condensed tannins reduce fecundity and total egg output of *H. contortus* in goats (Kahiya et al., 2003; Paolini et al., 2003). By consuming plants that are high in tannins, the hosts are reducing their future infection risk by limiting the number of eggs that enter the environment. Over time, the condensed tannins would decrease the species diversity within a particular group of hosts, or lower the mean intensity of those nematodes adversely affected by the chemical.

Niche overlap appears to be the dominant factor structuring the component community of impala. As in Holmes and Podesta (1968), hosts with similar ranges and diets are exposed to nearly the same parasites. For impala, significant overlap in local habitat occurs within the sexes, such that females congregating in clans harbor a component community different from the less social males. Additionally, the cost of territoriality in males, namely indiscriminate food consumption, exposes them to a greater array of infective stages, including those species commonly occurring in other ungulate hosts.

It is clear that age and sex of impala influence the structure of the parasite community. A combination of social organization and behavior is probably producing these differences. A comparison of impala infracommunities to those of the greater kudu reveal striking differences (Fellis et al., 2003). Those nematodes that are common in the impala are rare or occasional in the kudu, and vice versa. Both the diet and social organization of the kudu, a nongregarious browser (Estes, 1990), probably produce these differences. The wildebeest infracommunity (Horak et al., 1983) also includes species that infect both the kudu and impala. Of the 4 common species recovered from the wildebeest, *Trichostrongylus thomasi* and *O. columbianum* are common in the impala, whereas *Cooperia conochaeti* and *Haemonchus bedfordi* are rare. Although they are not ungulates, scrub hares (Boomker et al., 1997) show similar patterns. Five of the 6 nematodes infecting the hares also infect impala, i.e., *Cooperia hungi*, *Impalaia tuberculata*, *Trichostrongylus deflexus*, *T. falculatus*, and *T. thomasi*. Additionally, 4 of these 5 species have prevalences greater than 40%. None of the common species of the kudu infect wildebeests or scrub hares.

The various feeding preferences will expose the host to a specific set of infective larvae that are capable of migrating onto their food source. Thus, nematodes species that are most adept at dispersing up blades of grass will likely be rare in browsers, and vice versa. Of the mammals mentioned, kudu are browsers, impala are intermediate feeders, and wildebeest and scrub hares consume grass (Estes, 1990). It is not surprising then, that some of the common species of the intermediate feeding impala are also common or occasional in either browsing or grazing species. Furthermore, rough estimates of commonness or rarity of the nematodes of 2 browsers, the grey duiker and bushbuck (Boomker et al., 1986), show that they are most similar to the kudu.

Food preference is only 1 factor that shapes the infracommunities of antelope in KNP. Social organization, i.e., gregarious vs. nongregarious species, is another. As previously discussed, impala are gregarious and form herds. Living in herds increases the risk of repeated exposure to infective larvae (Altizer et al., 2003). Kudu, on the other hand, are much less social. Herds are formed, but the average number of kudu in these herds is much less than the average number of impala in a herd (Skinner and Smithers, 1990). Even though kudu are larger than impala, and have the potential to hold a greater number of nematodes (Halvorsen, 1986), the intensity of infection is only 20% that of the impala. Lack of repeated exposure may be causing the lower intensity levels.

Careful inspection of Boomker et al. (1986) reveals that component communities of different host species can be similar within a region. Describing the transmission dynamics within KNP requires an understanding of the factors that shape the component community of a host species (Fig. 2). First, preferred habitat and activity of a host will determine the species of parasites that can potentially infect a host. If the infective stages are not present or encountered, then that parasite will be absent from the host in that region. Second, food preference will dictate which infective stages are consumed. Infective larvae migrate onto and up certain types of vegetation better than others (Callinan and Westcott, 1986; Niezen et al., 1998). Those hosts preferentially consuming the infested plants are more likely to harbor a heavy infection. Third, the host does not come in contact with those infective larvae common on unpalatable vegetation. Thus, food preference not only affects the presence or absence of specific nematodes, but it also influences the relative abundance within the host. Finally, the last host factor that shapes the component community is social organization. The degree of gregarious behavior can often indicate the level of repeated exposure experienced by members of the herd (Altizer et al., 2003).

Attention to host factors is only a single dynamic in understanding parasite component communities. Within a habitat, there can be multiple host species that are infected by the same subset of parasites. The movement patterns within and between habitats promote the dispersal of infective stages, thus homogenizing the component communities of various host species. This is offset by variations in habitat and food preference, which inhibit successful species sharing. Consider a region with 6 host species living in 3 habitats (Fig. 3). Of the host species, 2 are pure grazers, 2 are pure browsers, and 2 are intermediate or mixed feeders. Within the same habitat, 2 grazers have the potential to share a larger number of parasite species than 2 host species with different feeding preferences. Moreover, differences in habitat preference restrict the number of parasite species shared between 2 browsers. Intermediate feeders are the link between browsers and grazers. They harbor species common to both, and can disperse infective stages so that browsers are exposed to the parasites of grazers, and vice versa.

Niche overlap, whether in diet or habitat, likely explains the

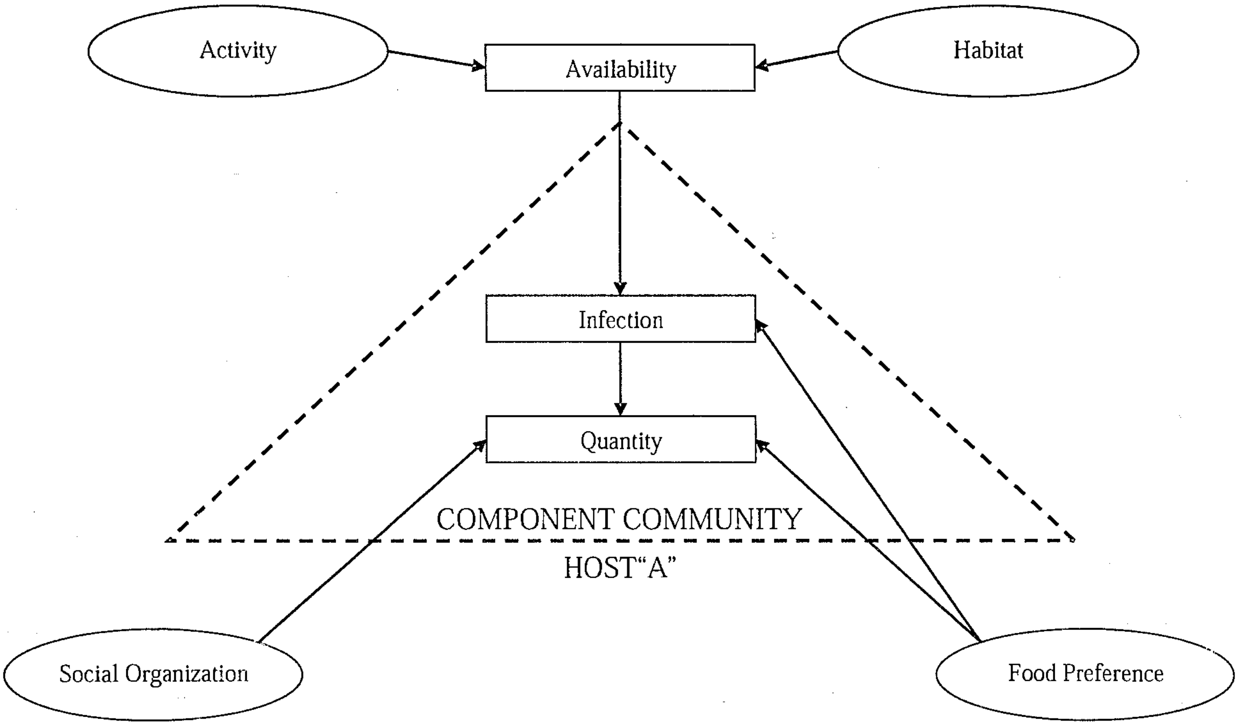

FIGURE 2. Diagram showing the determinants of the component community of a single host species. Both habitat preference and level of activity will determine the number of species that could be potentially encountered by the host. Infection requires that the parasite is present in the area and consumed by the host. The worm burden is controlled by food preference and social organization. Factors related to the host are placed in ovals.

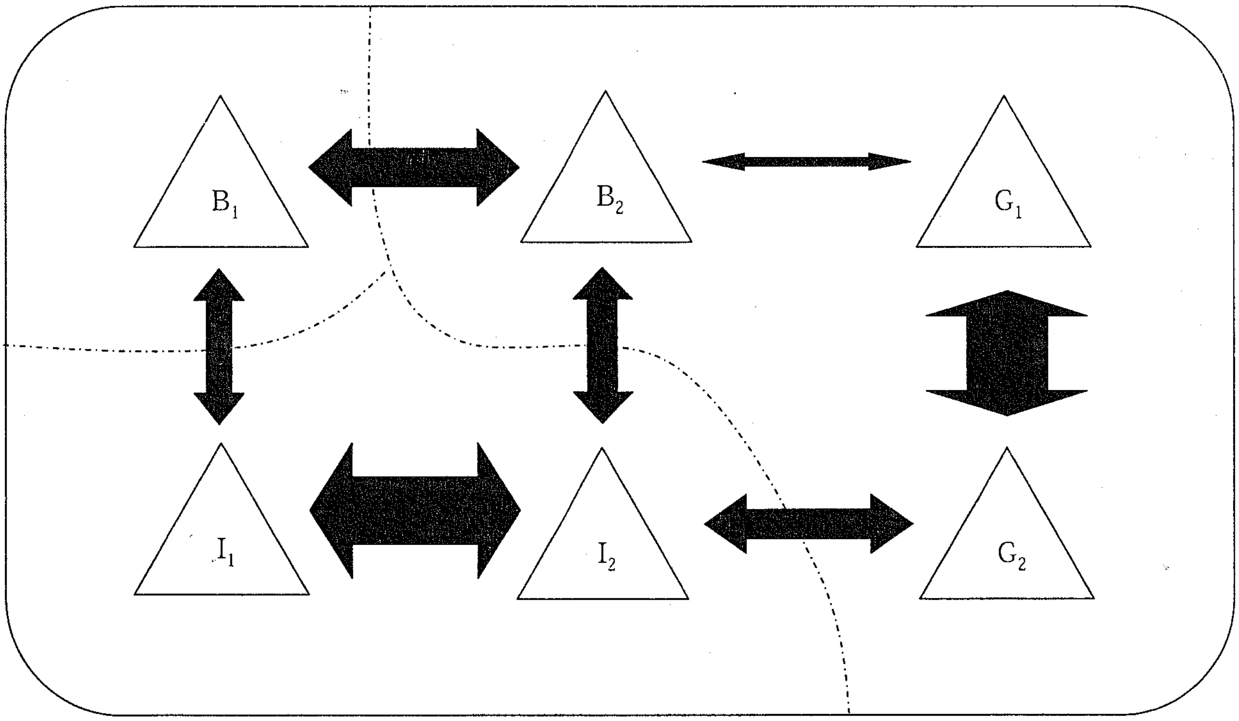

FIGURE 3. Concept of species sharing between different hosts (triangles) in various habitats (dashed line). The hosts include browsers (=B), grazers (=G), and mixed feeders (=I), with the subscript indicating differences in host species. Arrow thickness represents the relative amount of overlap in reference to those parasites infecting both host species.

patterns observed in the component communities of hosts from KNP. This idea has also been proposed for freshwater fishes (Nelson and Dick, 2002; Johnson et al., 2004). The latter authors concluded that dominance of parasite species in a compound community reflects the presence of specific host species and the degree of overlap of infected intermediate hosts in the definitive hosts' diet. For KNP, dietary overlap pertains to food preference, i.e., whether an animal is a browser, a grazer, or intermediate, and habitat dictates which hosts are present and contributing parasites to the compound community pool.

Transmission between host species is, therefore, likely occurring in KNP. With complete records of all antelope in KNP, we will likely see that certain nematode species are common in specific subsets of antelope. For example, *C. conochaeti* and *H. vegliai* may be common only in browsers, and accidental in grazing antelopes. *Trichostrongylus falculatus* may be common only in grazers (Horak, 1978). The common species of intermediate feeders probably include common species from both browsers and grazers. Variability in this pattern, such as the presence of "host-specific" nematodes, may arise from differences in habitat preference of the host (grassland vs. woodland habitat).

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