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ORIGINAL RESEARCH

Helminth parasites of impalas, *Aepyceros melampus*, in eastern southern Africa, collected during 1973 to 2007

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This paper summarises published and unpublished data on helminths collected systematically from 424 impalas at 11 localities in eastern southern Africa, from St. Lucia in KwaZulu-Natal (KZN) to the Tuli Block in north-eastern Botswana. It includes data on collections in the Kruger National Park (KNP) in the drought of 1982, and in 1992/93 following the 1991/92 drought. Thirty-three species of nematodes, plus six taxa identified only to the generic level, three taxa of trematodes, and three species of cestodes were collected. Helminth species richness was highest in the southern KNP and lowest in the Tuli Block. The prevalence and intensity of infection of several helminths also declined from KZN and the southern KNP to the drier areas in the north and west. With the exception of St. Lucia and Nylsvley, > 80% of the helminths collected at each locality were collected in the southern KNP. St. Lucia was the most dissimilar locality; of the 20 helminths collected, five were unique. Ten of 33 species of nematodes, the paramphistomines (Trematoda) and the cestode *Stilesia hepatica* were collected at seven or more localities. Six of the most common nematodes, *Cooperia hungi*, *Cooperioides hamiltoni*, *Impalaia tuberculata*, *Longistrongylus sabie*, *Strongyloides papillosus* and *Trichostrongylus deflexus* are primarily parasites of impalas in the southern KNP, whereas many of the helminths collected at only one or two localities are parasites of other hosts. Nematode burdens were increased in the drought affected impalas in 1982, but helminth burdens decreased in 1992/93 following a dry cycle.

Keywords: zooparasitic Nematoda, Cestoda, Trematoda, prevalence, distribution, drought

Introduction

Impalas, *Aepyceros melampus*, are medium-sized, lightly built antelope widespread in the eastern parts of Africa (Skinner & Chimimba 2005). In South Africa, impalas occur mainly in the provinces of Limpopo, Mpumalanga, North West, Gauteng, and the north-eastern KwaZulu-Natal (KZN).

According to Round (1968), two trematode and two cestode species, a larval cestode, 16 nematode species and a nematode genus occurred in impalas in South Africa. Most of these records were for parasites collected incidentally or during culling operations (Meeser 1952; Young & Wagener 1968). Since then, there have been a number of reports (Horak 1978; Anderson 1983; Boomker, Horak et al. 1989b; van Wyk & Boomker 2011) based on the systematic collection of the helminths of impalas that provide quantitative estimates of the prevalence and intensity of infection at various localities in South Africa. Negovetich et al. (2006) examined the infracommunities and component communities of nematodes infecting the impalas at three localities, Skukuza, Biyamiti and Crocodile Bridge, in the southern Kruger National Park (KNP) from 1980 to 1982, but did not discriminate between localities, nor consider the potential effects of the drought that occurred in 1982. Horak et al. (2023) re-examined the data from Skukuza and Biyamiti, and compared the differences in prevalence and intensity of infection in helminths between the two localities by age, sex and month.

In addition to the collections in the southern KNP in 1980 and 1982, IGH was able to collect helminths from impalas at Pafuri in the north of the KNP in 1977 and 1980, and Prof J Boomker from animals on the research farm 'Delftzyl' in Limpopo Province. We (IGH, LEOB) also collected helminths from impalas at Skukuza, Crocodile Bridge and Pafuri in 1992/93, at the end of, and after, the 1991/1992 drought. An unknown collector, whom we have been unable to trace, also provided collections of helminths from impalas in the Tuli Block (North Tuli and South Tuli) region of north-eastern Botswana. The collections in 1977 and 1980 at Pafuri, 1992/1993 in the KNP, at Delftzyl, and in the Tuli Block are unpublished, and as noted above, Negovetich et al. (2006) combined localities and years in their analyses, thus the collections from Crocodile Bridge in 1980 and in the southern KNP during the 1982 drought are also unpublished.

The unpublished collections, plus the previously published reports of Horak (1978), Anderson (1983), Boomker et al. (1989b), van Wyk and Boomker (2011) and Horak et al. (2023) provide information on the helminths of impalas throughout South Africa, from north-eastern KZN to the northern tip of the KNP and into north-eastern Botswana. The collections encompass a range of habitats, with annual rainfall ranging from approximately 900 mm in KZN to 300–400 mm in the north of the KNP and the Tuli Block. This paper compares the differences in helminth species prevalence and intensity of infection among the various

Figure 1: Localities in eastern southern Africa at which impalas were examined during 1973 to 2007. Locality 1 (Tuli Block), 2 (Northern Limpopo Province), 3 (Parfuri), 4 (Nylsvley Nature Reserve), 5 (Delftzyl), 6 (Skukuza), 7 (Byamiti), 8 (Crocodile Bridge), 9 (Nyala Game Ranch) and 10 (St. Lucia Nature Reserve). Grid references are listed in Table I

localities, and assesses the impact of the droughts of 1982 and 1991/92 in the KNP.

Materials and methods

Study areas

The localities (Figure 1), the vegetation type, and the number of and frequency with which the impalas were examined at each locality are presented in Table I. All of the localities are within the summer rainfall region of southern Africa. Rainfall is variable with wet cycles and dry cycles, and is subject to periodic droughts (Tyson 1978). The annual rainfall at Skukuza in the KNP over the period of all collections, including those of Anderson (1983) and van Wyk and Boomker (2011), is shown in Figure 2. The period contained two wet cycles, from 1972 to 1981, and 1993 to 2002, and two dry cycles, from 1982 to 1991/1992, and from 2003.

Parasite collection

The methodology for parasite collections in the published papers is described by the authors (Horak 1978; Anderson 1983; Boomker et al. 1989b; van Wyk & Boomker 2011; Horak et al. 2023). The methodology used for the unpublished collections at Pafuri, at Crocodile Bridge in 1980, in the 1982 and 1992/93 droughts, and at Defltzyl was described by Horak et al. (2023). We are unable to determine the exact methods by which the impala were processed for helminth recovery in the Tuli Block, but the identification of helminths and counting procedures were as described by Horak et al. (2023).

Effect of drought

The collections included two drought periods, the first in 1982, and the second in 1991/1992. The 1982 drought followed a year of low rainfall in 1981/1982, with below average rainfall in the winter and spring of 1982. This was preceded by a period of above average rainfall from 1971 to 1981 (Fig. 2). Drought-affected impalas were collected from October to December 1982 at Skukuza, Biyamiti and Crocodile Bridge in the southern KNP (Table I). Impalas that did not appear to be affected were also collected at Skukuza. The collections in 1992/1993 followed a period of below average rainfall from 1982 to 1992, with the lowest rainfall in 1991/1992 and slightly above average rainfall in 1992/1993. Impalas were collected at Skukuza, Crocodile Bridge and Pafuri (Table I) from February 1992, at the end of the dry year, until May 1993. Thus, the 1992/1993 collections not only included the end of the drought year, but also the recovery period in a year of above average rainfall.

Statistical methods

Factors of interest in the analysis of the data were the differences among localities and the effect of drought. However, it was not possible to compare directly among localities because only aggregate data was available for the helminth burdens in the Nyala Game Ranch (NGR) (Anderson 1983) and St. Lucia (Boomker et al. 1989b) in KZN. Individual animal data were available for the other localities, but the collections were independent and factors that potentially affect helminth burdens, such as age, month and sex (Horak et al. 2023), were not balanced across localities. Therefore, the data were analysed using exploratory data analysis techniques to describe patterns and trends, with extensive use of graphical analysis to assess differences.

Differences in prevalence were analysed using contingency tables with a χ^2 and logistic regression. For differences in the intensity of infection, the parasite count data were logarithmically transformed to reduce the inequality of variance created by overdispersion (Petney et al. 1990). The data were then analysed using analysis of variance. 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 compare among multiple groups. When factors such as age, sex and month potentially affected the interpretation, secondary analyses were conducted with restricted data sets to balance those factors when possible. For example, for the 1982 drought, drought-affected and non-drought-affected impalas were compared to age-sex matched controls from November and December 1980 at Skukuza. For the 1992/93 drought, only yearling males were collected at Skukuza; these were compared to yearling males collected at Skukuza in 1980. However, at Crocodile Bridge, yearling and adult males

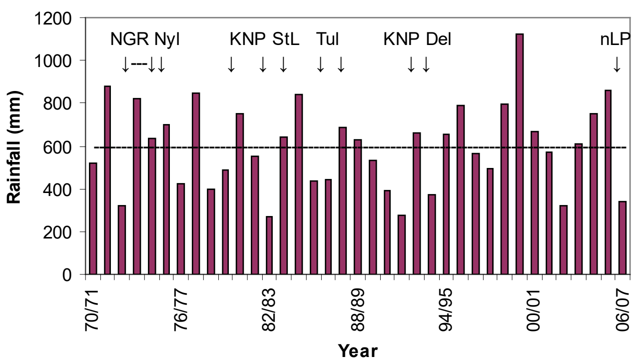

Figure 2: Annual rainfall at Skukuza in the KNP from 1970 to 2002. Arrows indicate the timing of the collections at the various localities. The horizontal line is the mean annual rainfall over the 32-year period. NGR, Nyala Game Ranch; Nyl, Nylsvley; KNP, Kruger National Park; StL, St. Lucia; Tul, Tuli Block; Del, Delftzyl; nLP, northern Limpopo Province

Table I: Grid references, altitudes, vegetation types, annual rainfall, time periods and numbers of impalas examined at the various localities

Locality Grid Reference; Altitude	Vegetation Type (Reference)	Annual Rainfall (mm)	Collection Period	Number of impalas; age/sex distribution
Skukuza (KNP) 24° 58′ S, 31° 36′ E; Alt. 262 m	Thickets of the Sabie and Crocodile Rivers (Gertenbach 1983)	≈ 600	Jan 1980–Dec 1980	3–7 impalas monthly (*n* = 49); 4 LF, 8 LM, 12 YM, 12 AF, 13 AM
			Nov 1982–Dec 1982	10 impalas monthly (*n* = 20); 2 LM, 3 YM, 7 AF, 7AM; 1 not recorded
			Mar 1992–Apr 1993	12 impalas in Mar 1992; YM. 3–6 impalas monthly thereafter (*n* = 74); YM
Biyamiti (KNP) 25° 06′–25° 28′S, 31° 25′–31° 39′E; Alt. 200–350 m	Mixed Bushwillow Woodlands (Gertenbach 1983)	600–700	Jan 1980–Dec 1980	3–6 impalas monthly (*n* = 47); 2 LF, 10 LM, 12 YM, 10 AF, 13 AM
			Nov 1982	4 impalas; 1 LM, 2 AM. 1 AF
Crocodile Bridge (KNP) 25° 22′ S, 31° 54′ E; Alt. 217 m	Marula/Knobthorn Savanna (Gertenbach 1983)	≈ 600	Jan 1980–Dec 1980	1 impala monthly (*n* = 12); AM
			Oct 1982	1 impala; AF
			Feb 1992	10 impalas; 5 YM, 5 AM
			May 1993	7 impalas; 5 AF, 2 AM
Pafuri (KNP) 23° 27′ S, 31° 19′ E; Alt. 305 m	Mopani Veld on Limpopo and Levubu Floodplains (Gertenbach 1983)	420	Aug 1977	12 impalas; 1 LF, 4 LM, 2 AF, 5 AM
			Jul 1980	4 impalas; 1 LM, 1 YM, 1 AF, 1 AM
			Mar 1992–Apr 1993	3 impalas at 2–3 month intervals (*n* = 21); 12 YM, 9 AM
Delftzyl (Limpopo Province) 24° 39′ S, 29° 16 E; Alt. 850 m	Mixed Bushveld, and small areas of Turf Thornveld (Acocks 1988)	500–600	Jul 1993–Jun 1994	1–3 impalas monthly (*n* = 20); 1 YF, 2 YM, 5 AF, 12 AM
Tuli Block (north-eastern Botswana) 22° 50′ S, 28° 00′ E; Alt. 520–670 m	Savanna, rocky outcrops, large trees on river banks	≈ 350 (northern portion)	May 1986–Nov 1986	4–7 impalas at 1–2 month intervals (*n* = 31); North: 4 F, 3M; South: 19 F, 5 M (age not provided)
			Sep 1988	15 impalas; North: 2 F; South: 13 F (age not provided)
Nylslvley Nature Reserve (Limpopo Province) 24° 29′S, 28° 42′E; Alt. 1100 m	Sour Bushveld (Acocks 1988)	625	Feb 1975–Feb 1976	2–4 impalas monthly (*n* = 36); 4 LF, 9 LM, 1 YF, 6 YM, 7 AF, 9 AM
Nyala Game Ranch (KZN) 28° 41′S, 31° 42′E; Alt. ≈200 m	Zululand Thornveld (Acocks 1988)	900	Mar 1973–Feb 1975	46 impalas; 8 L, 27 Y, 11 A (sex not provided)
St. Lucia Nature Reserve (KZN) 32° 30′S, 28° 47′E; Alt. <50 m	Zululand Palm Veld (Acocks 1988)	700	May 1984	2 impalas in St. Lucia Game Park; (age, sex not provided)
			August 1984	3 impalas in Charter's Creek; (age, sex not provided)
Northern Limpopo Province 22°40′–22°56′S, 28°02′–29°55′E	Soutpansberg: Mixed Bushveld (Acocks 1988)	300 (avg 326)	Aug 2007	3 impalas; (age, sex not provided)
	Musina: Thorn and Mopani veld (Acocks 1988)	500	June 2006, July 2007	5 impalas; (age, sex not provided)
	Lephalale (Acocks 1988)	178	June 2006	2 impalas; (age, sex not provided)

L, lamb (0–11 months old); Y, yearling (12–23 mo); A, adult (≥ 24 mo); F, female; M, male; KNP, Kruger National Park; KZN, KwaZulu-Natal; avg, average

were collected in February 1992 and adult males and females were collected in May 1993. These were compared to adult males, the only age-sex class collected, in 1980.

Impalas less than two years old were aged to month and were classed as lambs (0–11 months), yearlings (12–23 months) or adults (older than 24 months) in the analyses.

Results

The unpublished and published collections included 424 impalas. Thirty-three species of nematodes plus six taxa identified only to the generic level, three taxa of trematodes, and three species of cestodes were collected.

The localities at which the helminths were collected are shown in Table II, although not all helminths were collected at a given locality each time when there were collections in multiple years at that locality. Table III lists the prevalence and intensity of infection of the helminths, excluding the drought years of 1982 and 1992/93. Helminth species richness and similarity were highest in the southern KNP, with 23 species at Skukuza and Crocodile Bridge, and 24 species at Biyamiti (Table IV). Species richness was lowest in North Tuli (eight species), South Tuli (11

Table II: Helminths collected at the eleven localities

Locality	Skukuza	Biyamiti	Crocodile Bridge	Pafuri	North Tuli	South Tuli	Delftzyl	Nylsvley	Nyala Game Ranch	St. Lucia	Northern Limpopo
Nematodes											
Agriostomum gorgonis Le Roux, 1929			•				•				
Agriostomum sp.										•	
Bunostomum trigonocephalum (Rudolphi, 1808)				•							
Cooperia connochaeti Boomker, Horak & Alves, 1979	•	•	•	•							
Cooperia fuelleborni Hung, 1926	•	•	•	•					•	•	•
Cooperia hungi Mönnig, 1931	•	•	•	•	•	•	•	•		•	•
Cooperia neitzi Mönnig, 1932	•	•									
Cooperia yoshidai Mönnig, 1939										•	
Cooperia spp.										•	
Cooperioides hamiltoni (Mönnig, 1932)	•	•	•	•	•	•	•	•	•	•	•
Cooperioides hepaticae Ortlepp, 1938	•	•	•	•		•	•	•	•	•	•
Dictyocaulus viviparus (Bloch, 1782)										•	
Gaigeria pachyscelis Railliet & Henry, 1910	•	•	•	•					•	•	
Gongylonema pulchrum Molin, 1857								•			
Haemonchus bedfordi Le Roux, 1929	•	•							•		
Haemonchus contortus (Rudolphi, 1803)							•		•	•	
Haemonchus krugeri Ortlepp, 1964	•	•	•	•							•
Haemonchus placei Place, 1893								•			
Haemonchus vegliai Le Roux, 1929		•			•						
Impalaia tuberculata Mönnig, 1923	•	•	•	•	•	•	•	•	•	•	•
Longistrongylus namaquensis (Ortlepp, 1963)						•					
Longistrongylus sabie (Mönnig, 1932)	•	•	•	•			•	•	•		•
Longistrongylus schrenki Ortlepp, 1939						•				•	
Nematodirus spathiger (Railliet, 1896)			•								
Oesophagostomum columbianum Curtice, 1890	•	•	•	•	•	•	•	•	•		•
Oesophagostomum sp.										•	
Ostertagia sp.										•	
Pneumostrongylus calcaratus Mönnig, 1932	•	•	•						•		
Strongyloides papillosus (Wedl, 1856)	•	•	•	•			•	•	•	•	
Trichostrongylus angistris Boomker, 1986										•	
Trichostrongylus axei (Cobbold, 1879)								•	•		
Trichostrongylus colubriformis (Giles, 1892)			•				•	•	•		•
Trichostrongylus deflexus Boomker & Reinecke, 1989	•	•	•	•	•	•	•				•
Trichostrongylus falculatus Ransom, 1911	•	•	•	•			•	•	•		
Trichostrongylus instabilis (Railliet, 1893)										•	
Trichostrongylus thomasi Mönnig, 1932	•	•	•	•	•					•	
Trichostrongylus spp.										•	
Trichuris globulosa (von Linstow, 1901)	•	•	•	•			•		•		
Trichuris sp.								•			
Trematodes											
Paramphistominae gen. sp.	•	•	•	•		•		•	•	•	
Fasciola gigantica Cobbold, 1855								•			
Schistosoma mattheei Veglia & Le Roux, 1929	•	•	•								
Cestodes											
Moniezia benedeni (Moniez, 1879)	•	•		•	•	•	•				
Moniezia expansa (Rudolphi, 1810)	•	•	•					•	•		•
Stilesia hepatica Wolfhügel, 1903	•	•	•	•		•	•		•		•

Table III: Prevalence and intensity of infection of the helminths collected from 287 impalas at the eleven localities, excluding the drought years of 1982 and 1992/1993. n = number of impalas examined. The data are presented as prevalence (%); mean intensity of infection (range). Range was not calculable at the Nyala Game Ranch and St. Lucia because individual animal data are not available

Locality	Skukuza (n = 49)	Biyamiti (n = 47)	Crocodile Bridge (n = 12)	Pafuri (n = 16)	North Tuli (n = 9)	South Tuli (n = 37)	Delftzyl (n = 20)	Nylsvley (n = 36)	Nyala Game Ranch (n = 46)	St. Lucia (n = 5)	Northern Limpopo (n = 10)
Nematodes											
Total adult nematodes	98.0; 5505 (150–36060)	100.0; 4158 (25–29113)	100.0; 2812 (603–6296)	100.0; 2081 (281–6050)	100.0; 696 (150–1600)	91.9; 3244 (130–11375)	100.0; 1205 (60–6126)	100.0; 4043 (14–18560)	100.0; 20504	100.0; 2129	100.0; 522 (125–850)
Agriostomum gorgonis	-	-	16.7; 2 (2,2)	-	-	-	40.0; 17 (5–40)	-	-	-	-
Agriostomum sp.	-	-	-	-	-	-	-	-	-	20.0; 25	-
Bunostomum trigonocephalum	-	-	-	25.0; 1.3 (1–3)	-	-	-	-	-	-	-
Cooperia connochaeti	2.0; 125 (125)	10.6; 16 (10–50)	8.3; 675 (675)	50.0; 353 (150–600)	-	-	-	-	-	-	-
Cooperia fuelleborni	12.2; 375 (100–850)	10.6; 170 (50–325)	33.3; 590 (100–1560)	-	-	-	-	-	97.8; 2857[a] Adults: 1321	40.0; 42	10.0; 75 (75)
Cooperia hungi	87.8; 835 (50–3180)	93.6; 1064 (25–6645)	83.3; 835 (75–2000)	100.0; 394 (50–1500)	77.8; 193 (10–410)	78.4; 2254 (10–8760)	65.0; 252 (10–1089)	97.2; 583 (2–2981)	-	40.0; 102	90.0; 281 (25–500)
Cooperia yoshidai	-	-	-	-	-	-	-	-	-	40.0; 553	-
Cooperia spp.	-	-	-	-	-	-	-	-	-	40.0; 942	-
Cooperioides hamiltoni	91.8; 618 (10–4405)	89.4; 530 (50–2575)	100.0; 454 (25–1015)	93.6; 454 (25–1900)	44.4; 163 (30–490)	83.8; 581 (30–2100)	65.0; 74 (1–325)	88.9; 730 (1–4560)	91.3; 771	100.0; 59	20.0; 137.5 (75–200)
Cooperioides hepaticae	83.7; 155 (5–685)	83.0; 99 (5–465)	75.0; 49 (5–225)	68.8; 34 (5–79)	-	10.8; 12.5 (5–30)	5.0; 15 (15)	77.8; 64 (1–492)	91.3; [b]	40.0; 42.5	20.0; 15 (10–20)
Dictyocaulus viviparus	-	-	-	-	-	-	-	-	-	20.0; 18 (18)	-
Gaigeria pachyscelis	81.6; 6.2 (1–31)	74.5; 9.0 (1–38)	91.7; 12.2 (1–42)	6.3; 1 (1)	-	-	-	-	97.8; 96[a] Adults: 24	20.0; 77 (77)	-
Gongylonema pulchrum	-	-	-	-	-	-	-	5.6; 2 (1–3)		-	-
Haemonchus bedfordi	6.1; 50 (25–75)	8.5; 51 (2–75)	-	-	-	-	-	-	100.0; 1137[a] Adults: 303	-	-
Haemonchus contortus	-	-	-	-	-	-	60.0; 48 (10–120)	-	4.3; [b]	100.0; 675	-
Haemonchus krugeri	57.1; 103 (5–410)	70.2; 108 (6–585)	33.3; 35 (8–55)	-	-	-	-	-	-	-	20.0; 325 (250–400)
Haemonchus placei	-	-	-	-	-	-	-	83.3; 84 (1–450)	-	-	-
Haemonchus vegliai	-	6.4; 2.3 (2–3)	-	-	11.1; 10 (10)	-	-	-	-	-	-
Impalaia tuberculata	81.6; 579 (25–6110)	85.1; 491 (25–3135)	58.3; 115 (25–210)	62.5; 295 (25–850)	33.3; 23.3 (10–50)	43.2; 153 (20–560)	80.0; 1063 (1–4127)	88.6; 1715 (4–9022)	100.0: 1483[a] Adults: 626	40.0; 898	50.0; 140 (25–325)
Longistrongylus namaquensis	-	-	-	-	-	5.4; 85 (50–120)	-	-	-	-	-
Longistrongylus sabie	83.7; 150 (10–700)	83.0; 125 (19–395)	66.7; 66 (25–200)	62.5; 53 (25–125)	-	-	75.0; 94 (1–371)	75.0; 134 (1–769)	97.8; 465[a] Adults: 408	-	10.0; 50 (50)

Locality	Skukuza (*n* = 49)	Biyamiti (*n* = 47)	Crocodile Bridge (*n* = 12)	Pafuri (*n* = 16)	North Tuli (*n* = 9)	South Tuli (*n* = 37)	Delftzyl (*n* = 20)	Nylsvley (*n* = 36)	Nyala Game Ranch (*n* = 46)	St. Lucia (*n* = 5)	Northern Limpopo (*n* = 10)
Longistrongylus schrenki	-	-	-	-	-	21.6; 147 (2–540)	-	-	-	60.0; 202	-
Oesophagostomum columbianum	71.4; 69 (1–686)	78.7; 41 (1–161)	100.0; 37 (2–256)	75.0; 16 (1–64)	22.2; 15 (10–20)	37.8; 70 (20–320)	45.0; 22.4 (1–101)	66.7; 17 (1–71)	95.7; 180 [a] Adults: 155	-	50.0; 90 (25–250)
Oesophagostomum sp.	-	-	-	-	-	-	-	-	-	40.0; 25	-
Ostertagia sp.	-	-	-	-	-	-	-	-	-	40.0; 77	-
Pneumostrongylus calcaratus	83.7 [c]	83.0 [c]	100.0 [c]	-	-	-	-	-	97.8 [c]	-	-
Strongyloides papillosus	85.7; 352 (10–935)	87.2; 457 (25–1585)	83.3; 318 (50–650)	81.3; 523 (25–1375)	-	-	5.0; 6 (6)	5.6; 4 (3–5)	100.0; 5138	20.0; 450 (450)	-
Trichostrongylus angistris	-	-	-	-	-	-	-	-	-	20.0; 1 (1)	-
Trichostrongylus axei	-	-	-	-	-	-	-	50.0; 142 (10–518)	93.5; 281	-	-
Trichostrongylus colubriformis	-	-	-	-	-	-	15.0; 1.3 (1–2)	86.1; 1113 (1–8058)	100.0; 11033	-	20.0; 88 (25–150)
Trichostrongylus deflexus	89.8; 2815 (50–28425)	93.6; 1368 (25–14340)	100.0; 738 (100–2800)	81.3; 501 (50–1725)	100.0; 460 (90–1590)	83.8; 712 (50–3000)	5.0; 10 (10)	-	-	-	40.0; 44 (25–75)
Trichostrongylus falculatus	6.1; 167 (50–350)	21.3; 88 (50–250)	16.7; 88 (50–125)	-	-	-	30.0; 84 (1–325)	50.0; 177 (10–480)	30.4; 417	-	-
Trichostrongylus instabilis	-	-	-	-	-	-	-	-	-	20.0; 10 (10)	-
Trichostrongylus thomasi	87.8; 406 (10–1820)	78.7; 328 (25–2560)	83.3; 222 (25–405)	-	11.1; 10 (10)	-	-	-	-	60.0; 40	-
Trichostrongylus spp.	-	-	-	-	-	-	-	-	-	80.0; 81	-
Trichuris globulosa	57.1; 5.6 (1–16)	8.5; 1.3 (1–2)	8.3; 2 (2)	6.3; 1 (1)	-	-	5.0; 10 (10)	-	76.1; 25	-	-
Trichuris sp.	-	-	-	-	-	-	-	2.8; 1	-	-	-
Trematodes											
Paramphistominae gen. sp.	46.9; 256 (3–3195)	78.7; 1097 (1–6970)	16.7; 18.5 (7–30)	6.3; 865 (865)	-	8.1; 24 (2–50)	-	50.0; 45 (2–285)	89.1; [b]	20.0; 1 (1)	-
Fasciola gigantica	-	-	-	-	-	-	-	2.8; 4 (4)	-	-	-
Schistosoma mattheei	12.2; 10 (5–20)	6.4; 12 (5–25)	8.3; 5 (5)	-	-	-	-		-	-	-
Cestodes											
Monieza benedeni	4.1; 1 (1)	6.4; 2.4 (2–3)	-	18.8; 2 (1–3)	11.1; 2 (2)	13.5; 2.8 (1–7)	15.0; 1.7 (1–2)	-	-	-	-
Monieza expansa	2.0; 1 (1)	-	-	-	-	-	-	25.0; 1.6 (1–3)	6.5; [b]	-	10.0; 5 (5)
Stilesia hepatica	8.2; 25; (15–35)	4.3; 25 (20–30)	33.3; 14 (5–20)	18.8; 2.7 (1–6)	-	-	10.0; 1 (1–1)	-	15.2; [b]	-	10.0; 7 (7)

[a] Includes L4 larvae; adult intensity of infection estimated based on number of adults in Table 2 of Anderson (1983) and prevalence of infection in Table 3; [b] Number of parasites not reported; [c] Prevalence based on the presence of eggs at Skukuza, Biyamiti and Crocodile Bridge, and lung lesions at the Nyala Game Ranch

Table IV: Number of helminth species, including paramphistomines and nematode genera, collected at each locality (bold, bottom diagonal) and the number of species shared with the other localities

Locality	Biyamiti	Skukuza	Crocodile Bridge	Pafuri	North Tuli	South Tuli	Delftzyl	Nyala Game Ranch	Nylsvley	St. Lucia	Northern Limpopo
Biyamiti	**24**	23	20	18	8	9	12	15	10	9	11
Skukuza		**23**	20	18	7	9	12	15	10	9	11
Crocodile Bridge			**23**	17	6	6	12	15	10	8	12
Pafuri				**19**	7	8	12	12	9	9	10
North Tuli					**8**	6	6	3	4	3	5
South Tuli						**11**	8	6	6	5	7
Delftzyl							**15**	11	9	6	8
Nyala Game Ranch								**18**	11	8	8
Nylsvley									**16**	6	8
St. Lucia										**20**	5
Northern Limpopo											**12**

species) and the northern Limpopo Province (nLP; 12 species). At most localities, > 80% of the species were also collected at Skukuza and Biyamiti. The greatest dissimilarities in species were at St. Lucia and Nylsvley where only 45% and 62.5% of the species that were collected at Skukuza and Biyamiti were present, patterns that were consistent in comparison to the other localities. Five of the 20 helminths at St. Lucia, *Cooperia yoshidai*, *Dictyocaulus viviparus*, *Trichostrongylus angistris*, *Trichostrongylus instabilis* and the genus *Ostertagia*, were only collected there, as were three of the 16 species at Nylsvley, *Gongylonema pulchrum, Haemonchus placei* and *Fasciola gigantica*.

All of the species collected at North Tuli were collected at Biyamiti, as were nine of the 11 species collected at South Tuli and 11 of 12 in the nLP. However, < 55% of the species collected at North Tuli and South Tuli were collected at the Nyala Game Ranch (NGR), Nylsvley and St. Lucia.

Nematodes

All of the impalas (n = 424) were infected with adult nematodes except one new-born lamb at Skukuza and three females of unknown age at South Tuli.

Ten of the 33 species of nematodes identified may be considered widespread as they were collected at seven or more localities. *Cooperioides hamiltoni* and *Impalaia tuberculata* were collected at all eleven localities, *Cooperia hungi, Cooperioides hepaticae* and *Oesophagostomum columbianum* were collected at ten, and *Longistrongylus sabie*, *Strongyloides papillosus* and *Trichostrongylus deflexus* were collected at eight, while *Cooperia fuelleborni* and *Trichostrongylus falculatus* were collected at seven.

Sixteen species had more restricted distributions. *Haemonchus bedfordi* and *Haemonchus contortus* were collected at three localities, *Agriostomum gorgonis*, *Cooperia neitzi*, *Haemonchus vegliai*, *Longistrongylus schrenki* and *Trichostrongylus axei* were collected at two localities, and *Bunostomum trigonocephalum*, *C. yoshidai*, *D. viviparus*, *G. pulchrum*, *H. placei*, *Longistrongylus namaquensis*, *Nematodirus spathiger*, *T. angistris* and *T. instabilis* were only collected at one locality.

Nematode burdens

With the exception of the lungworms, *P. calcaratus* and *D. viviparus*, all of the nematodes were in the gastrointestinal tract. The prevalence of *P. calcaratus* was ≥ 83% in the southern KNP based on the presence of eggs, and 98% in the NGR based on the presence of lesions in the lungs. *Dictyocaulus viviparus* was collected from one impala (20%) at St. Lucia.

The arithmetic mean intensity of infection of adult gastrointestinal nematodes was 4–5 times higher in the NGR than at Skukuza and Biyamiti, while the arithmetic mean at St. Lucia was similar to that at Pafuri (Table III). The prevalence of 11 of the 14 species of gastrointestinal nematodes at the NGR was > 90%, and the intensity of infection of eight species was > 2 times the intensity at Skukuza and Biyamiti. The log-transformed mean intensity of infection did not differ significantly between Skukuza, Biyamiti, Crocodile Bridge, Nylsvley, South Tuli and Pafuri ($p > 0.05$), but was lower at North Tuli, Delftzyl and the nLP ($p = 0.001$).

The 10 most widespread species of nematodes accounted for > 90% of the nematodes in the KNP, Tuli Block and Delftzyl, 80.2% in the nLP, 72.8% at Nylsvley, 43.0% in the NGR, and 27.4% at St. Lucia. *Trichostrongylus deflexus*, *C. hungi* and *C. hamiltoni* accounted for > 66% of the gastrointestinal nematodes in the southern KNP and > 95% in the Tuli Block. They were also common at Pafuri, and *C. hungi* and *C. hamiltoni* were common at Delftzyl and Nylsvley, while *C. hungi* was the most numerous species in the nLP. The prevalence of *T. deflexus* was > 80% in the KNP and Tuli Block, but only 40% in the nLP and 5% at Delftzyl. The intensity of infection in the nLP and at Delftzyl was < 10% of that in the KNP and Tuli Block. *Trichostrongylus deflexus* was not collected in the NGR, St. Lucia or Nylsvley. *Trichostrongylus colubriformis* was the most numerous adult nematode at the NGR, accounting for 53.8% of the adult gastrointestinal nematodes, and the second most numerous at Nylsvley (23.7%), but was only collected from three impalas (17.6%) at Crocodile Bridge in 1992/93, three (15.0%) at Delftzyl and two (20%) in the nLP. The arithmetic mean intensity of infection was 11 033 in the NGR, 1 113 at Nylsvley, 88 in the nLP, and < 10 at Delftzyl and Crocodile Bridge.

The prevalence of *C. hungi* was > 80% in the KNP, Nylsvley and the nLP, and 78.0% in the Tuli block, but was only 65% at Delftzyl and 40% in St. Lucia; *C. hungi* was not collected at the NGR. The intensity of infection was highest in the southern KNP and South Tuli, and lowest in the nLP and Delftzyl ($p < 0.001$). The arithmetic mean was lowest at St. Lucia. The prevalence of *C. hamiltoni* was > 80% in the KNP, South Tuli, Nylsvley, the NGR and St. Lucia, 65% at Delfzyl, 44.4% at North Tuli and 20% in the nLP. The intensity of infection did not differ among localities in the KNP, South Tuli and Nylsvley, but was significantly lower in the nLP and at North Tuli and Delftzyl ($p < 0.001$). The arithmetic mean intensity of infection in the NGR was similar to Nylsvley, while that at St. Lucia was similar to Delftzyl.

Other common species in the southern KNP were *I. tuberculata* (2.4–10.1% of adult gastrointestinal nematodes) and *S. papillosus* (5.6–9.6%). *Impalaia tuberculata* was the most numerous species at Delftzyl (70.5%) and Nylsvley (36.5%), and second most numerous at St. Lucia (16.9%). The prevalence of adult *I. tuberculata* was > 80% at Delftzyl, Biyamiti, Skukuza, the NGR and Nylsvley. At the other localities, the prevalence ranged from approximately 40% at St. Lucia and the Tuli Block to 62.5% at Pafuri. The intensity of infection was highest in the NGR, and at Skukuza, Biyamiti, Pafuri, Delftzyl and Nylsvley, and lowest in the Tuli Block and nLP. *Strongyloides papillosus* was the second most numerous nematode in the NGR (25.1% of adult gastrointestinal nematodes) and at Pafuri (20.4%). It accounted for 4.3% of the gastrointestinal nematodes at St. Lucia and < 0.1% at Delftzyl and Nylsvley, and was not collected in the Tuli Block or nLP. The prevalence of *S. papillosus* was 100% at the NGR, > 80% in the KNP, 20% at St. Lucia, and 5% at Delftzyl and Nylsvley. The arithmetic mean intensity of infection in the NGR (5138) was 10-fold higher than in the KNP (318–523) and St. Lucia (450), but only four at Nylsvley and six at Delftzyl.

Even though they were widespread, *C. fuelleborni*, *C. hepaticae*, *L. sabie*, *O. columbianum* and *T. falculatus* normally accounted for less than 2.5% of the nematode burden. The exceptions were *C. fuelleborni*, which accounted for 7.0% of the nematodes at Crocodile Bridge in 1980 and 6.3% in the NGR, and *L. sabie*, which accounted for 5.8% of the nematodes at Delftzyl. The prevalences of *C. hepaticae*, *L. sabie* and *O. columbianum* were > 90% in the NGR, and the arithmetic mean intensities of infection of *L. sabie* and *O. columbianum* in the NGR were more than double the intensities in the other localities. The prevalences of *C. hepaticae*, *L. sabie* and *O. columbianum* were 62.5–100.0% in the KNP and Nylsvley. The prevalences of *C. hepaticae* and *O. columbianum* were significantly higher in the KNP and Nylsvley than at Delftzyl and the nLP ($p > 0.001$); *L. sabie* was not collected in the Tuli Block or St. Lucia, *C. hepaticae* was not collected at North Tuli, and *O. columbianum* was not collected in St. Lucia. The logarithmic mean intensity of infection of *C. hepaticae* did not differ between Skukuza, Biyamiti and Nylsvley, but was significantly lower at South Tuli, Delftzyl and in the nLP ($p < 0.001$). The logarithmic mean intensity of infection of *L. sabie* did not differ among localities, while the intensity of infection of *O. columbianum* was significantly higher at South Tuli and the nLP than at Pafuri, North Tuli, Delftzyl and Nylsvley.

Cooperia fuelleborni and *T. falculatus* were not collected at Pafuri in 1977/80, but were collected there in 1992/93. Neither species was collected in the Tuli Block, while *C. fuelleborni* was not collected at Delftzyl and Nylsvley, and *T. falculatus* was not collected in the nLP or St. Lucia. The prevalence of *C. fuelleborni* was > 90% in the NGR, and the arithmetic mean intensities of infection of both species were more than double the intensities in the other localities. Outside of the NGR, the prevalence of *C. fuelleborni* was ≤ 40%. The intensity of infection did not differ between Skukuza, Biyamiti and Crocodile Bridge ($p = 0.25$), but was higher than at Pafuri, St. Lucia and the nLP. The prevalence of *T. falculatus* was ≤ 50% at all localities and the logarithmic intensity of infection did not differ among localities ($p > 0.2$).

Gaigeria pachyscelis, *T. thomasi* and *T. globulosa* were collected at the four localities in the KNP and two other localities. The prevalence of *G. pachyscelis* was ≥ 75% in the southern KNP and NGR, 6.3% at Pafuri and 20% at St. Lucia; it accounted for < 0.4% of the nematodes in the KNP and NGR, and 1.5% at St. Lucia. The prevalence of *T. thomasi* was > 75% in the southern KNP and 60% at St. Lucia, but only 11% at North Tuli; it was not collected at Pafuri in 1977/80, but was collected there in 1992/93. *Trichostrongylus thomasi* accounted for approximately 6.5% of the gastrointestinal nematodes in the southern KNP, but ≤ 1.2% at North Tuli and St. Lucia, and at Pafuri in 1992/93. *Trichuris globulosa* was collected in the KNP, NGR and Delftzyl. The prevalence was > 50% at Skukuza and the NGR, and ≤ 10% at the other localities. The arithmetic mean intensity of infection was 25 at the NGR, but ≤ 10 at the other localities.

Cooperia connochaeti was only collected in the KNP. The prevalence was ≤ 10.6% in the southern KNP, and 50% at Pafuri. It accounted for < 2% of the adult nematodes in the southern KNP and 3.4% at Pafuri. The prevalence of *Haemonchus krugeri* was 57.1% at Skukuza, 70.2% at Biyamiti, 33.3% at Crocodile Bridge and 20% in the nLP. It accounted for < 2% of the adult nematodes in the southern KNP and 12.5% in the nLP. *Haemonchus krugeri* was not collected at Pafuri in 1977/80, but was collected there in 1992/93.

The 15 remaining species were collected at three or fewer localities. Nine were relatively uncommon, with prevalences < 50% and accounting for < 1% of the nematode burden. Of the others, *C. yoshidai*, with a prevalence of 40%, accounted for 10.4% of the nematodes at St. Lucia, while the prevalence of *H. placei* was 83.3% at Nylsvley where it accounted for 1.5% of the nematodes. The prevalence of *H. contortus* was 100% at St. Lucia and 60% at Delftzyl, but only 4.3% in the NGR. It was the most numerous nematode at St. Lucia (31.7% of gastrointestinal nematodes), and accounted for 2.4% of the nematodes at Delftzyl. The prevalence of *H. bedfordi* was 100% in the NGR, but < 10% at Skukuza and Biyamiti. The prevalence of *L. schrenki* was 60% at St. Lucia, where it accounted for 5.7% of the nematodes,

Table V: Prevalence and intensity of infection of the helminths in the drought year of 1982 and the 1980 controls. *n* = number of impalas examined. The data are presented as prevalence (%); arithmetic mean intensity of infection (range)

Locality	**Skukuza**			**Biyamiti**		**Crocodile Bridge**	
Group	**Drought-Affected (*n* = 10)**	**Non–Drought-Affected (*n* = 10)**	**1980 Controls (*n* = 10)**	**Drought-Affected (*n* = 4)**	**1980 Controls (*n* = 4)**	**Drought -Affected (*n* = 1)**	**1980 Controls (*n* = 2)**
Nematodes							
Total adult nematodes	100; 23045 (4832–52490)	100; 8879 (171–21126)	100; 9150 (1487 –36060)	100; 8664 (2626–20260)	100; 10774 (3206–29113)	100; 94565	100.0; 3731 (1165–6296)
Cooperia connochaeti	-	-	-	25; 25 (25)	25; 25 (25)	-	-
Cooperia fuelleborni	50; 12.4 (2–50)	30; 12.7 (2–25)	-	-	-	100; 3707	-
Cooperia hungi	100; 5216 (332–9516)	100; 1332 (16–3312)	90; 722 (50–2275)	100; 3124 (747–8582)	100; 2599 (1030–6645)	100; 40498	100; 1038 (75–2000)
Cooperia neitzi	-	10; 75 (75)	-	50; 39 (27–50)	-	-	-
Cooperioides hamiltoni	100; 3965 (491–7779)	100; 913 (64–2737)	100; 935 (250–4405)	100; 770 (67–1794)	100; 801 (385–1375)	100; 18184	100; 405 (385–425)
Cooperioides hepaticae	90; 763 (10–3709)	90; 65 (5–196)	70; 254 (15–595)	75; 24 (2–45)	75; 90 (55–115)	100; 50	100; 35 (5–65)
Gaigeria pachyscelis	30; 34.3 (25–50)	70; 29.3 (1–75)	90; 4.3 (1–10)	25; 25 (25)	75; 6.7 (2–14)	100; 100	100; 2.5 (1–4)
Haemonchus krugeri	100; 1710 (314–3620)	90; 555 (1–1942)	60; 68.5 (3–135)	100; 703 (103–1329)	100; 273 (125–595)	100; 6307	50; 55 (55)
Impalaia tuberculata	90; 3481 (109–8400)	100; 1237 (5–3935)	70; 343 (255–895)	100; 1549 (238–3117)	100; 1184 (450–3135)	100; 5058	50; 185 (185)
Longistrongylus sabie	100; 475 (93–1192)	100; 192 (6–478)	90; 196 (10–700)	100; 344 (10–895)	100; 144 (10–395)	100; 3363	50; 25 (25)
Oesophagostomum columbianum	80; 247 (1–1025)	50; 215 (25–475)	50; 12.8 (2–36)	75; 108 (25–225)	100; 59 (4–161)	100; 100	100; 14.5 (9–20)
Strongyloides papillosus	60; 249 (6–825)	80; 299 (31–551)	100; 164 (75–825)	100; 451 (75–800)	100; 240 (100–575)	100; 451	100; 350 (250–450)
Trichostrongylus deflexus	100; 5699 (300–25596)	100; 3353 (4–9253)	90; 6612 (600–28425)	100; 1165 (605–2449)	100; 4445 (660–14340)	100; 8443	100; 1450 (100–2800)
Trichostrongylus falculatus	70; 212 (26–1125)	40; 32 (2–75)	20; 200 (50–350)	50; 27 (26–28)	75; 133 (50–250)	100; 260	50; 125 (125)
Trichostrongylus thomasi	100; 1592 (31–6000)	100; 684 (3–2066)	100; 606 (125–1820)	100; 415 (103–1295)	75; 1133 (230–2560)	100; 8337	100; 240 (75–405)
Trichuris globulosa	20; 38 (25–50)	20; 389 (100–678)	70; 7.0 (2–16)	-	25; 2 (2)	-	50; 2 (2)
Trematodes							
Paramiphistominae gen. sp.	10; 501 (501)	60; 875 (1–4145)	50; 151 (52–421)	75; 537 (99– 1172)	75; 1113 (37–3003)	-	-
Schistosoma mattheei	-	10; 5 (5)	30; 11.7 (5–20)	50; 7.5 (5–10)	-	-	-
Cestodes	-			-	-	-	-
Monieza benedeni	-	10; 3 (3)	10; 1 (1)	-	-	-	-
Monieza expansa	-	10; 5 (5)	-	50; 1.5 (1–2)	-	-	-
Stilesia hepatica	40; 26 (1–100)	30; 1.7 (1–3)	10; 20 (20)	-	25; 20 (20)	100; 1 (1)	50; 15 (15)

and 26.1% at South Tuli where it accounted for 1.1% of the nematodes. *Trichostrongylus axei* was relatively common at the NGR and Nylsvley with prevalences of 93.5% and 50% respectively, but accounted for < 2.0% of the adult nematodes; it was not collected at the other localities.

Coinfections

Excluding the NGR and St. Lucia for which individual animal data were not available, the mean number of gastrointestinal nematode species per impala was 7.7 (range 0–14), with a high

Table VI: Prevalence and intensity of infection of the helminths in 1992/1993 versus the 1980 controls. *n* = number of impalas examined. The data are presented as prevalence (%); arithmetic mean intensity of infection (range of intensity)

Locality	Skukuza		Crocodile Bridge		Pafuri	
	1992/93 (*n* = 74)	**1980 (*n* = 12)**	**1992/93 (*n* = 17)**	**1980 (*n* = 12)**	**1992/93 (*n* = 21)**	**1977/80 (*n* = 16)**
Nematodes						
Total adult nematodes	100.0; 1778 (1–5523)	100.0; 5840 (1856–10052)	100.0; 667 (42–2625)	100.0; 2812 (603–6296)	100.0; 2330 (400–5040)	100.0; 2081 (281–6050)
Cooperia fuelleborni	6.8; 20 (20–20)	16.7; 525 (200–850)	64.7; 174 (2–700)	33.3; 590 (100–1560)	14.3; 27 (20–40)	-
Cooperia hungi	91.9; 465 (1–1484)	91.7; 1030 (225–1800)	88.2; 322 (15–1164)	83.3; 835 (75–2000)	95.2; 1080 (40–2760)	100.0; 394 (50–1500)
Cooperioides hamiltoni	91.9; 273 (1–705)	100.0; 572 (10–965)	76.5; 162 (1–480)	100.0; 454 (25–1015)	100.0; 512 (60–1960)	93.8; 454 (25–1900)
Cooperioides hepaticae	63.5; 22 (1–68)	100.0; 312 (50–685)	41.2; 11 (5–20)	75.0; 49 (5–225)	-	68.8; 34 (5–79)
Gaigeria pachyscelis	9.5; 1.3 (1–2)	100.0; 7.9 (1–31)	29.4; 12.2 (1–20)	91.7; 12.2 (1–42)	4.8; 2 (2)	6.3; 1 (1)
Haemonchus krugeri	47.3; 70 (1–220)	75.0; 120 (3–410)	47.1; 41 (20–121)	33.3; 35 (8–55)	9.5; 20 (20–20)	-
Impalaia tuberculata	81.1; 354 (1–1320)	91.7; 548 (25–1225)	58.8; 74 (5–283)	58.3; 115 (25–210)	90.5; 192 (20–680)	62.5; 295 (25–850)
Longistrongylus sabie	54.1; 55 (20–177)	91.7; 161 (10–375)	58.8; 32 (1–104)	66.7; 66 (25–200)	76.2; 76 (20–200)	62.5 53 (25–125)
Nematodirus spathiger	-	-	17.6; 6 (1–16)	-	-	-
Oesophagostomum columbianum	44.6; 76 (20–820)	83.3; 71 (7–260)	17.6; 30 (10–50)	100.0; 37 (1–256)	65.4; 78 (20–160)	75.0; 16 (1–64)
Strongyloides papillosus	70.3; 284 (20–980)	100.0; 299 (125–475)	41.2; 59 (10–150)	83.3; 318 (50–650)	61.9; 86 (20–280)	81.3; 523 (25–1375)
Trichostrongylus colubriformis	-	-	17.6; 6 (1–16)	-	-	-
Trichostrongylus deflexus	91.9; 512 (20–2840)	100.0; 2383 (1005–4665)	29.4; 79 (10–190)	100.0; 738 (100–2800)	90.5; 452 (60–1080)	81.3; 501 (50–1725)
Trichostrongylus falculatus	27.0; 45 (20–140)		11.8; 11 (5–16)	16.7; 88 (50–125)	19.0; 110 (45–253)	-
Trichostrongylus thomasi	41.9; 40 (1–200)	100.0: 414 (150–800)	23.5; 6.3 (2–10)	83.3; 222 (25–405)	38.1; 75 (32–160)	-
Trichuris globulosa	9.5; 17 (2–30)	100.0; 5.5 (1–10)	-	8.3; 2 (2)	-	6.3; 1 (1)
Trematodes						
Paramphistominae gen. sp.	-	-	5.9; 1 (1)	-	-	-
Cestodes						
Monieza expansa	-	-	17.6; 1 (1–1)	-	-	-
Stilesia hepatica	9.5; 5.9 (1–13)	16.7; 25 (15–35)	17.6; 12 (1–25)	33.3; 14 (5–20)	-	18.8; 2.7 (1–6)

of 9.8 (range 0–14) in the southern KNP in 1980, and a low of 3.5 (range 0–6) in the Tuli Block and nLP. There was a high degree of coinfection, particularly among the more widespread and numerous species, *C. hungi*, *C. hamiltoni*, *I. tuberculata*, *S. papillosus* and *T. deflexus*. However, the prevalence of coinfections was generally similar to that expected based on the product of the individual prevalences.

Trematodes and cestodes

Three taxa of trematodes, paramphistomines, and *Fasciola gigantica* and *Schistosoma mattheei*, and three species of cestodes, *Monieza benedeni*, *Monieza expansa* and *Stilesia hepatica*, were collected in the surveys. None were collected in all localities, and with the exception of the paramphistomines, the prevalence was typically < 25% and the intensities of infection were ≤ 25. The prevalence of paramphistomines was >

75% at Biyamiti and the NGR, and the arithmetic mean intensity of infection at Biyamiti was 1 097; paramphistomines were not collected at North Tuli, Delftzyl or the nLP. *Schistosoma mattheei* was only collected in the southern KNP and *F. gigantica* was only collected at Nylsvley. The cestode, *M. benedeni* was collected at Pafuri, the Tuli Block and Delftzyl, while *M. expansa* was collected at the NGR, Nylsvley and the nLP. Both species were collected at Skukuza and Biyamiti (Table II), but from different individuals. *Stilesia hepatica* was not collected at North Tuli, Nylsvley or St. Lucia (Table II). There was no association between *S. hepatica* and *C. hepaticae* (Kappa = –0.012; $p = 0.72$).

Effect of drought

The intensity of infection of adult nematodes in the drought-affected impalas in 1982 was significantly higher than in the 1980 matched controls at Skukuza and Crocodile Bridge ($p = 0.003$), but did not differ at Biyamiti ($p = 0.88$). The increased intensity of infection at Skukuza and Crocodile Bridge reflected the increased intensities of infection of *C. hungi*, *C. hamiltoni*, *G. pachyscelis*, *H. krugeri*, *I. tuberculata*, *L. sabie*, *O. columbianum* and *T. globulosa*, and the increased prevalence of *H. krugeri* (Table V). The intensities of infection of *G. pachyscelis*, *H. krugeri*, *I. tuberculata* and *O. columbianum* were also increased in the non-drought-affected impalas. In contrast, there was no increase in the intensities of infection of *S. papillosus*, *T. deflexus*, *T. falculatus* and *T. thomasi*.

In 1992/93 (Table VI), the intensity of infection of adult nematodes at Skukuza and Crocodile Bridge was less than in 1980 ($p < 0.001$). The difference reflected declines in the prevalences of *C. hepaticae*, *O. columbianum*, *S. papillosus*, *T. deflexus* and *T. thomasi*, and the intensities of infection of *C. hungi*, *C. hamiltoni*, *C. hepaticae*, *L. sabie*, *S. papillosus*, *T. deflexus* and *T. thomasi*. At Pafuri, the burden of adult nematodes did not differ significantly between 1977/80 and 1992/93 ($p = 0.21$). In 1992/93, there were increases in the intensity of infection of *C. hungi* ($p = 0.02$) and *O. columbianum* ($p = 0.004$), but these were offset by the decrease in the intensity of infection of *S. papillosus* ($p < 0.001$). The intensity of infection in 1992/93 did not differ between Skukuza and Pafuri. The intensity of infection was highest at both localities in May–June 1992 and declined in 1993 after the spring/summer rains.

The three most numerous nematodes in the southern KNP in 1980, *C. hungi*, *C. hamiltoni* and *T. deflexus*, accounted for > 66% of the gastrointestinal nematodes. They accounted for approximately the same proportion (> 64%) in the 1982 drought-affected impalas and in 1992/93 at Skukuza and Crocodile Bridge, but only for 58.4% in the drought-affected impalas at Biyamiti in 1982. At Pafuri, *C. hungi*, *C. hamiltoni* and *T. deflexus* accounted for 83.7% of the gastrointestinal nematodes in 1992/93 versus 58.9% in 1980. At all localities, *C. hungi* accounted for a higher proportion of the gastrointestinal nematodes in 1982 and in 1992/93 than in 1980, while the proportion of *T. deflexus* declined in the drought years. *Agriostomum gorgonis*, *H. bedfordi* and *H. vegliai* were not collected in the southern KNP in1982, while *C. neitzi* was collected at Skukuza and Biyamiti (Table V). In 1992/93, *C. connochaeti* and *H. bedfordi*, were not collected at Skukuza and *A. gorgonis*, *C. connochaeti* and *T. globulosa* were not collected at Crocodile Bridge, while *N. spathiger* and *T. colubriformis* were. At Pafuri, *B. trigonocephalum*, *C. connochaeti*, *C. hepaticae* and *T. globulosa* were only collected in 1977/80 and *C. fuelleborni*, *H. krugeri*, *T. falculatus* and *T. thomasi* were only collected in 1992/93.

In 1982, the prevalences and intensities of infection of the trematodes and cestodes did not differ from 1980. In 1992/93, only one (5.9%) impala at Crocodile Bridge was infected with paramphistomines; none were collected at Skukuza or Pafuri. No *S. mattheei* or *M. benedeni* were collected in 1992/93, and only three impalas were infected with *M. expansa* at Crocodile Bridge. The prevalence of *S. hepatica* was lower in 1992/93 than in 1980 ($p = 0.05$), but the intensity of infection did not differ.

Discussion

The surveys of impala helminths in eastern South Africa and north-eastern Botswana show a mosaic of infections. Ten species of identified nematodes, plus the paramphistomines and the cestode *S. hepatica* were collected at seven or more of the localities and were considered widely distributed. Nine species of nematodes, the trematode *S. mattheei* and the cestodes *M. benedeni* and *M. expansa* had more restricted distributions and were collected at three to six localities. The remaining 14 species of nematodes and the trematode *F. gigantica* were only collected at one or two localities.

Helminth species richness was highest in the southern KNP and lowest in the Tuli Block. Five of the six species of nematodes collected at both North and South Tuli, *C. hungi*, *C. hamiltoni*, *I. tuberculata*, *O. columbianum* and *T. deflexus*, are widespread species. Other widespread species collected at seven or more localities, such as *C. fuelleborni*, *L. sabie*, *S. papillosus* and *T. falculatus*, were not collected in the Tuli Block, while *C. hepaticae* and the cestode *S. hepatica* were not collected at North Tuli. Among the remaining helminths, *G. pachyscelis* was only collected in the KNP and KZN; the prevalence was > 75% in the southern KNP and NGR, but only 6% at Pafuri. *Trichostrongylus thomasi* accounted for 6–9% of the nematodes in the southern KNP, but < 1.2% at North Tuli and St. Lucia. *Pneumostrongylus calcaratus* was collected in the southern KNP and NGR, and *S. mattheei* was only collected in the southern KNP.

The nematode burden was highest in the NGR and southern KNP, and lowest in the north and west at North Tuli, Delftzyl and the nLP. This was caused by the lower intensities of infection of *C. fuelleborni*, *C. hungi*, *C. hamiltoni*, *I. tuberculata*, *L. sabie*, *S. papillosus* and *T. globulosa*, as well as the lower prevalences of *C. hepaticae*, *G. pachyscelis* and *O. columbianum*.

The decreasing helminth species richness, nematode burden, and prevalences and intensities of infection of several nematodes from the southern KNP and the NGR to the Tuli Block, Delftzyl and nLP appear to be related to annual rainfall, which ranged from 900 mm per annum in the NGR to approximately 350 mm per annum in the Tuli Block and nLP. Drier conditions will reduce the environmental survival of the free-living stages of directly transmitted nematodes, and the survival and distribution of the intermediate hosts of indirectly transmitted helminths, such as *P. calcaratus* and the trematodes and cestodes.

South Tuli was an anomaly in the relationship between intensity of infection and rainfall, primarily because of the high intensity of infection in 1986. There are two possible explanations. First, 1986 was the second of two years of below average rainfall, and the higher intensity of infection in 1986 than in 1988 may reflect the short-term effect of drought and increase in the intensity of infection of gastrointestinal nematodes as seen in the drought-affected impalas in the southern KNP in 1982. The second explanation may be the age-sex distribution of the 1986 sample, in which there was a mix of sexes from May to August, but only females in October and November. At Skukuza and Biyamiti in 1980, there was a marked increase in the intensity of infection of nematodes in adult female impalas relative to the other age-sex classes from November to December (Horak et al. 2023). This was attributed to a periparturient relaxation of resistance in the females.

The 10 most widespread species of nematodes accounted for > 90% of the nematodes in the KNP, Tuli Block and at Delftzyl, with *T. deflexus*, *C. hungi* and *C. hamiltoni* the most numerous species in the southern KNP and Tuli Block. These three species were also common at Pafuri, and *C. hungi* and *C. hamiltoni* were common at Delftzyl and Nylsvley. In the nLP, *C. hungi* was the most numerous species. *Impalaia tuberculata* was the most numerous species at Delftzyl and Nylsvley, and the second most numerous species at St. Lucia and the nLP, while *S. papillosus* was the second most numerous at Pafuri and the NGR. Even though they were widespread, *C. hepaticae*, *L. sabie*, *O. columbianum* and *T. falculatus* seldom accounted for more than 2.5% of the nematode burden.

Trichostrongylus colubriformis was the most numerous nematode in the NGR and second most numerous at Nylsvley. It appears to replace *T. deflexus*. However, the collections in the NGR and at Nylsvley were from 1973 to 1976 (Anderson 1983; Horak 1978) and *T. deflexus*, which closely resembles *T. colubriformis*, was not described until 1989 (Boomker & Reinecke 1989).

Cooperia hungi was also not collected in the NGR, although Anderson (1983) reported it from the Hluhluwe Game Reserve in KZN, and it was collected at St. Lucia. The prevalence of *C. hungi* was > 75% at most localities, and it accounted for 13.6–59.3% of the gastrointestinal nematodes; it was the most numerous nematode at South Tuli in 1986 and in the nLP. At St. Lucia, the prevalence was 40% and it accounted for < 2% of the nematodes. As noted above, there was an increased intensity of infection of *C. hungi* in the drought-affected impalas in 1982. In 1992/93, the intensity of infection was increased at Pafuri, and even though the intensity of infection declined at Skukuza and Crocodile Bridge, the decline was less than for other species and *C. hungi* accounted for a higher proportion of the gastrointestinal nematodes. Interestingly, Boomker et al. (1991) did not collect any *C. hungi* from nyalas, *Tragelaphus angasii*, in north-eastern Natal in 1983/84 at the end of a wet cycle, but Boomker et al. (1996) reported an overall prevalence of 29.3% and arithmetic mean intensity of infection of 186 in 1991 at the end of a dry cycle. Thus, whereas for many nematodes the distribution and burden appear to be limited by low rainfall, *C. hungi* may be adapted to drier conditions.

St. Lucia was the most dissimilar locality, with the lowest proportion of widespread species and highest proportion of unique species. *Haemonchus contortus* was the most numerous nematode, followed by *I. tuberculata* and *C. yoshidai*. The intensities of infection of the widespread nematodes, *C. hungi* and *C. hamiltoni*, were lower than at most other localities, and *L. sabie*, *O. columbianum*, *T. deflexus* and *T. falculatus*, were not collected there, although Boomker et al. (1989b) list *Oesophagostomum* sp. in impalas, and *O. columbianum* was collected from reedbuck, *Redunca arundinum*, in the reserve. Several of the helminths collected at St. Lucia, *C. yoshidai*, *D. viviparus, T. angistris, T.* i*nstabilis* and the genus *Ostertagia*, were not collected at the other localities, or were only collected at one or two, i.e. *H. contortus* and *L. schrenki. Haemonchus contortus*, *C. yoshidai*, *D. viviparus* and *L. schrenki* were common parasites of reedbuck in the reserve (Boomker et al. 1989b).

Host assemblage is another factor that may influence helminth species richness and burden. In a comparative analysis of the gastrointestinal nematode burdens of herbivores in the south-central KNP (Horak et al. 2021), impalas had the highest nematode burden and species richness of the antelope (impalas, blue wildebeest, *Connochaetes taurinus*, and kudus, *Tragelaphus strepsiceros*). Three nematodes, *C. hamiltoni*, *H. krugeri* and *L. sabie* were only collected from impalas. To this list we may add *C. hepaticae*, which was not collected from the other antelope (Boomker et al. 1989a; Horak et al. 1983) and other hosts, warthogs, *Phacochoerus africanus* (as *Phacochoerus aethiopicus*), (Horak et al. 1988) and scrub hares, *Lepus saxatilis* (Boomker et al. 1997). Impalas were also the main hosts of *C. hungi*, *I. tuberculata* and *S. papillosus*, while the main hosts of *T. deflexus* were impalas and scrub hares. With the exception of *H. krugeri* which was only collected in the KNP and nLP, the nematodes of which impalas were the main hosts in the southern KNP are widespread and usually among the most numerous species.

Amongst the antelope (Horak et al. 2021), three genera of nematodes, *Cooperia, Cooperioides* and *Haemonchus*, exhibited host specificity, with *C. hungi, C. hamiltoni*, *C. hepaticae* and *H. krugeri* associated with impalas, *Cooperia acutispiculum*, *C. neitzi* and *H. vegliai* associated with kudus, and *C. connochaeti* and *H. bedfordi* with wildebeest. *Cooperia connochaeti*, *H. bedfordi* and *H. vegliai* were also collected from impalas in 1980, and *C. neitzi* was collected from impalas in the 1982 drought; none were collected in 1992/93. With the exception of *C. connochaeti* at Pafuri in 1980, the prevalence of these species was < 10%, suggesting that they were incidental infections.

A number of helminths, *F. gigantica*, *H. contortus*, *H. placei*, *G. pulchrum* and *T. axei*, collected from impalas at the NGR or Nylsvley were not collected in the KNP, or were rarely collected, i.e. *T. colubriformis*. All of these are parasites of domestic stock (Reinecke 1983). The NGR had been converted from a cattle ranch to a game farm approximately nine years prior to Anderson's (1983) collections, and the Nylsvley Nature Reserve had a herd of cattle (Horak 1978). *Fasciola gigantica* was also collected from an impala in north-eastern Eswatini in a reserve that had previously been a cattle ranch (Gallivan et al. 1996). *Haemonchus contortus* was collected from 60% of the impalas at Delftzyl and

T. colubriformis was collected from 15%. Both species were also parasites of indigenous goats on the farm, with prevalences of 92% for *H. contortus* and 27% for *T. colubriformis* (Boomker et al. 1994).

Horak et al. (2021) postulated that because impalas are intermediate feeders they would be exposed to nematodes infecting both browsers (kudus) and grazers (wildebeest). The widespread distribution of impalas throughout eastern South Africa also exposes them to a range of helminths infecting other antelope and domestic hosts. Thus, while impalas are primary hosts to several helminths, they are also infected by helminths that infect several other species and contribute to the helminth species richness of impalas.

Effect of drought

The response to drought conditions at Skukuza and Crocodile Bridge differed between 1982 and 1992/93, with an increase in nematode burdens in 1982 and a decrease in 1992/93. These patterns were similar to those reported for ticks collected at the same time (Horak et al. 1995, 2003). Horak et al. (1995, 2003) attributed the differences in tick response to differences in the droughts and impala populations. The collections in the 1982 drought were made at the end of the dry season following a period of low rainfall beginning in February 1982. This was preceded by a period of above average rainfall from 1971 to 1981 (Fig. 2), and the impala population in the Skukuza area was approximately 4 500. In contrast, the 1992/93 collections began at the end of the 1991/92 drought and encompassed a year of above average rainfall in 1992/93. The collections followed a period of below average rainfall from 1982 to 1992, and the impala population in the Skukuza area was approximately 1 000.

The differences in responses suggest both an acute and long-term response to drought. The acute response was an increase in nematode burdens and the intensities of infection of several nematode species, *C. hungi*, *C. hamiltoni*, *G. pachyscelis*, *H. krugeri*, *I. tuberculata*, *L. sabie*, *O. columbianum* and *T. globulosa*. The increased nematode burdens in the non-drought affected impalas support the hypothesis that the drought was a factor. However, whether the increased nematode burden contributed to the poor condition of the drought-affected impalas, or whether the nematode burden was a result of their condition cannot be determined.

In 1992/93, the decline in nematode populations at Skukuza and Crocodile Bridge occurred in several species, *C. hungi*, *C. hamiltoni*, *C. hepaticae*, *L. sabie*, *O. columbianum*, *S. papillosus*, *T. deflexus, T. thomasi* and *T. globulosa*. For some, *C. hamiltoni, C. hepaticae, L. sabie*, *S. papillosus* and *T. globulosa*, the overall prevalence and/or intensity of infection exhibited a decrease from the higher rainfall localities in the southern KNP and KZN to the lower rainfall localities in the Tuli block and nLP. The distributions of other species such as *C. fuelleborni*, *G. pachyscelis* and *T. thomasi* were restricted primarily in the southern KNP and KZN. While *C. hungi*, *C. hamiltoni, C. hepaticae, G. pachyscelis* and *L. sabie* are primarily parasites of impalas, the other nematodes, *S. papillosus*, *T. deflexus*, *T. falculatus* and *T. thomasi*, infect a range of hosts (Horak et al. 2021). The decline in impala populations from 1982 to 1992/93 coincided with the population declines of several ungulate species in the KNP beginning in the mid-1980s (Ogutu & Owen Smith 2005). Thus, the helminth burden of impalas may be affected, not just by the alternate hosts available, but also by both the population density of the impalas and the alternate hosts.

In contrast to Skukuza, there was little or no difference in the nematode burdens relative to 1980 at Biyamiti in 1982, or relative to 1977/80 at Pafuri in 1992/93. The lack of a statistically significant difference between the drought-affected impalas at Biyamiti in 1982 and 1980 controls may be the result of small sample sizes and high variance within the samples. While there wasn't a difference between years in the burdens at Pafuri, there was a shift in species as *C. connochaeti*, *C. hepaticae* and *T. globulosa* were not collected in 1992/93 and there was a decrease in the intensity of infection of *S. papillosus* ($p < 0.001$). These were largely replaced by *C. hungi*, which may be more tolerant of drier conditions.

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Conflict of interest

The authors declare they have no conflicts of interest that are directly or indirectly related to the research.

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Compliance with ethical guidelines

The authors declare that this submission is in accordance with the principles laid down by the Responsible Research Publication Position Statements as developed at the 2nd World Conference on Research Integrity in Singapore, 2010.

Ethical approval

All applicable institutional, national and international guidelines for the care and use of animals were followed.

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