Onderstepoort J. vet Res., 54, 71–78 (1987)

STUDIES ON THE PARASITES OF ZEBRAS. V. NEMATODES OF THE BURCHELL'S AND HARTMANN'S MOUNTAIN ZEBRAS FROM THE ETOSHA NATIONAL PARK, SOUTH WEST AFRICA/NAMIBIA

ROSINA C. KRECEK[1], R. K. REINECKE[1] and F. S. MALAN[2]

ABSTRACT

KRECEK, ROSINA C., REINECKE, R. K. & MALAN, F.S. 1987. Studies on the parasites of zebras. V. Nematodes of the Burchell's and Hartmann's mountain zebras from the Etosha National Park, South West Africa/Namibia. *Onderstepoort Journal of Veterinary Research*, 54, 71–78 (1987)

Nine Burchell's and 6 Hartmann's mountain zebras were culled during the 3 climatic periods characteristic of the Etosha National Park, South West Africa/Namibia, and were examined for helminths. The Burchell's zebras ranged in age from 4½ to 19 years and the mountain zebras from 3½ to 13 years. Twenty-five species of nematodes, belonging to the families Atractidae, Strongylidae, Oxyuridae, Onchocercidae and Habronematidae, were recovered. Of the family Cyathostominae, the following species were the most numerous in the Burchell's zebras: *Cyathostomum montgomeryi* (7 120–67 042), *Cylicocyclus triramosus* (11–34 540), *Cylicostephanus minutus* (4 698—40 019) and *Cylindropharynx* sp.(? *intermedia*) (3 591–40 018). The atractids present were: *Crossocephalus viviparus* (20–5 045 212) and *Probstmayria vivipara* (5 140–3 801 300). Three of the above cyathostome species were also most abundant in mountain zebras: *Cylicocyclus triramosus* (54–19 782), *Cylicostephanus minutus* (555–12 396) and *Cylindropharynx* sp. (? *intermedia*) (3–5 325).

New reports include *Cylicostephanus longiconus* in the Burchell's zebras and *Cyathostomum alveatum*, *Cyathostomum montgomeryi*, *Cylicostephanus bidentatus* and *Draschia megastoma* in the mountain zebra.

The overwintering of 4th stage cyathostomes in the gut walls and their emergence which differ in the 2 hosts, are discussed.

INTRODUCTION

The Etosha National Park is the habitat of both Burchell's *(Equus burchelli antiquorum)* and Hartmann's mountain zebra *(Equus zebra hartmannae)*, where they share some of the same grazing. With the exception of *Equus burchelli*, which is designated to species, the early host-parasite checklists (Mönnig, 1928: Le Roux, 1932) group all the zebras together, regardless of species. Scialdo-Krecek, Reinecke & Biggs (1983) reported on the seasonal prevalence of the internal parasites of Hartmann's mountain zebra in central SWA/Namibia, while Scialdo, Reinecke & De Vos (1982) reported on those of Burchell's zebra in the Kruger National Park. Etosha, moreover, presented a unique study. Firstly, it gave the opportunity to compare parasites from 2 zebra host species sharing the same locality and, secondly, to study the parasites from these 2 hosts during the 3 climatic periods which occur in Etosha.

MATERIALS AND METHODS

Study area

Nine burchell's and 6 Hartmann's mountain zebras were culled near Otjovasandu (19° 15′ S, 14° 31′ E), in the west of the Etosha National Park and in the central area near Okaukuejo (19° 8′ S, 15° 55′ E) (Fig. 1).

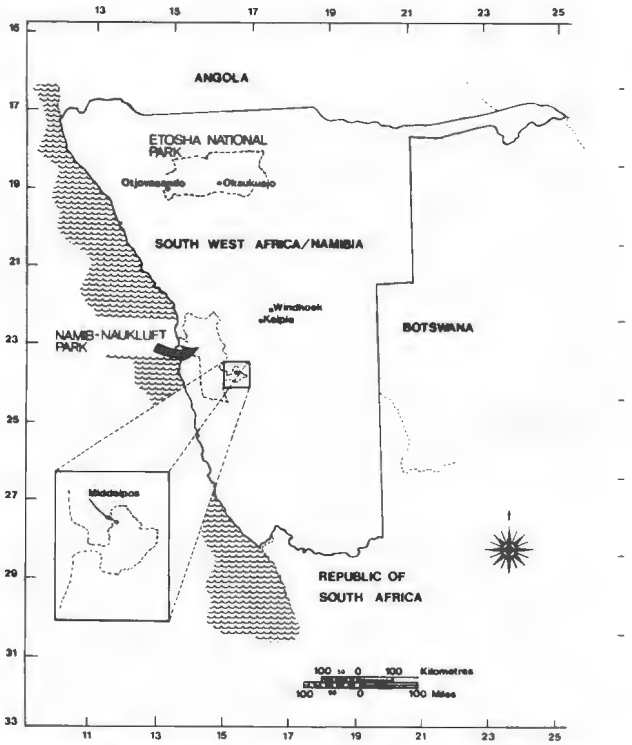

FIG. 1 South West Africa/Namibia, showing Etosha National Park in the North

FIG. 2 An area typical of Otjovasandu

FIG. 3 An area typical of Okaukuejo

[1] Department of Parasitology, Faculty of Veterinary Sciene, Private Bag X04, University of Pretoria, Onderstepoort 0110

[2] Hoechst Research Farm, P.O. Box 124, Malelane 1320

Received 16 September 1986—Editor

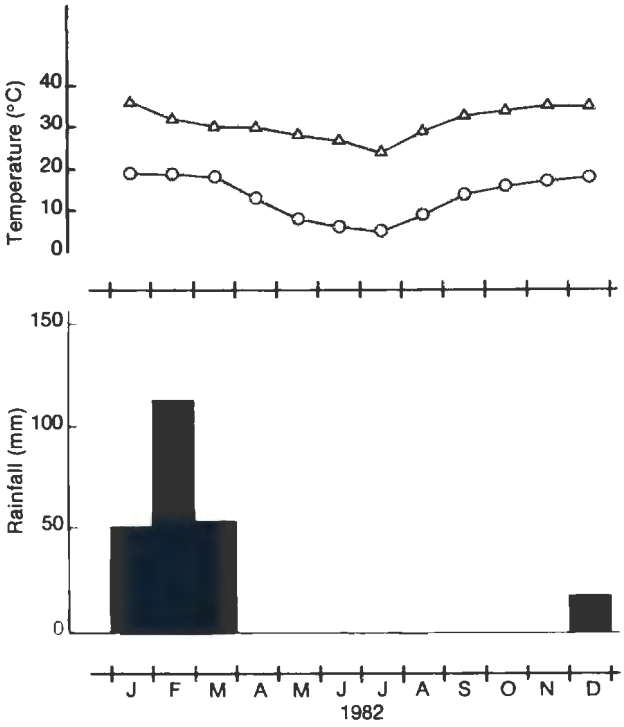

FIG. 4 Mean monthly maximum (△) and minimum (○) temperatures at Okaukuejo and total monthly rainfall at Otjovasandu in the Etosha National Park for 1982

The Etosha National Park (23 000 km^2) encompasses 2 major vegetation types: saline desert with a dwarf shrub savanna fringe, and Mopane savanna (Giess, 1971). Typical areas of Otjovasandu and Okaukuejo are illustrated in Fig. 2 and 3.

Sources of water for the zebras are both natural and artificial. Water-holes surround the Etosha Pan following rains, and man-made water-holes, providing water during dry periods, have been constructed along the perimeter of the pan.

Rainfall

Otjovasandu

The total annual rainfall at Otjovasandu for 1982 was 235 mm. No rain fell during 8 of the latter 9 months of the year.

The predicted long-term rainfall for this area is 300–350 mm per annum (Department of Water Affairs, SWA/Namibia, unpublished data, 1977). Temperature data, which were not available from Otjovasandu, were recorded from Okaukuejo (Fig. 4).

Okaukuejo

The total annual rainfall recorded at Okaukuejo in 1982 was 333 mm and no rain fell from May—August (Fig. 5). The predicted rainfall for this area is 400–450 mm per annum (Department of Water Affairs, SWA/Namibia, unpublished data, 1977).

Animals studied

Walter (1973), cited by Berry (1980), identifies 3 climatic periods at Etosha:

Wet and hot (1 January to 30 April)

Dry and cold (1 May to 31 August)

Dry and hot (1 September to 31 December).

Two Burchell's and 2 Hartmann's mountain zebras at Otjovasandu and 1 Burchell's near Okaukuejo were culled in each of the 3 seasons in 1982, that is, March, July and November.

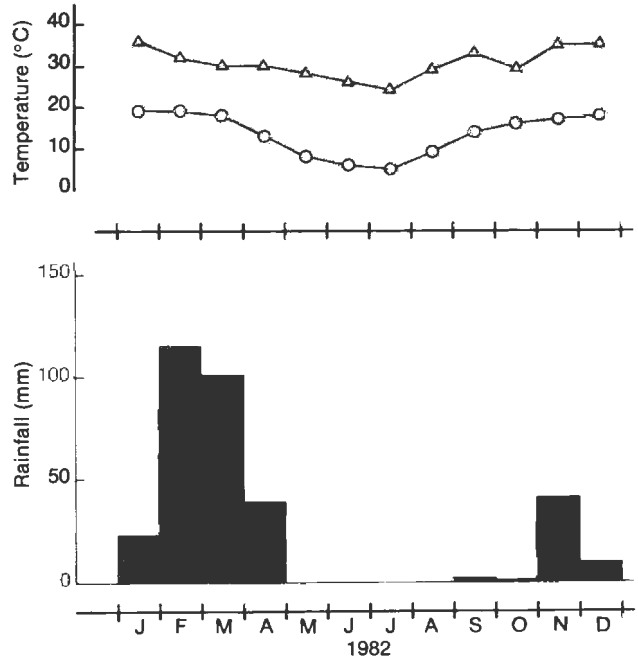

FIG. 5 Mean monthly maximum (△) and minimum (○) temperatures and total monthly rainfall at Okaukuejo in the Etosha National Park for 1982

Age

The Burchell's (B) zebras were divided into 2 age groups:

Five adult zebras aged 4,5–6,5 years and 4 old zebras aged 8,5–19 years.

The mountain (M) zebras were also divided according to age:

Three adult zebras aged 3,5–4,5 years and 3 old zebras aged 12–13 years.

Helminth collection

On 2 occasions, 2 zebras from Otjovasandu were shot and transported from 4–10 h to the Okaukuejo Veterinary Laboratory. A walk-in cooler with movable block allowed 1 zebra to be stored in a cool room, while necropsy on the other zebra was in progress. The method of collection of helminths from the zebra has been described by Malan, Reinecke & Scialdo (1981 a, b) and Scialdo-Krecek *et al.* (1983).

Identification of nematode species

Species were identified and recorded separately. The 5th stages and the sexually mature adults (A) were determined to the species level, while the 4th larval stage (L_4) was recorded as Habronematidae, Cyathostominae and *Triodontrophorus* spp.

RESULTS

The total nematode burdens included the families Strongylidae, Oxyuridae, Onchocercidae, Atractidae and Habronematidae (Tables 2–5). The mean nematode burdens and prevalence of cyathostomes in the intestinal tract of the Burchell's zebras are shown in Fig. 6, while the site distribution of the cyathostomes is illustrated in Fig. 7. The same information for the mountain zebras is presented in Fig. 8 & 9.

Twenty-five nematode species were recovered and divided as follows: 13 Cyathostominae, 4 Strongylinae, 4 Habronematidae, 1 Onchocercidae, 1 Oxyuridae and 2 Atractidae. The Atractidae had the highest burdens.

Sixteen *Habronema zebrae*, recovered from B6, are not included in Table 4.

TABLE 1 Descriptions used in the identification of nematodes in Burchell's and mountain zebras

	AUTHORS															
	Boulenger (1920a) & (1920b)	Cram (1924)	Ihle (1925)	Kotlán (1919)	Le van Hoa (1962)	Leiper (1911)	Lichtenfels (1975)	Looss (1900)	Ortlepp (1962)	Popova (1955)	Popova (1958)	Scialdo-Krecek (1983b)	Scialdo-Krecek & Malan (1984)	Theiler (1923)	Yeh (1959)	Yorke & Macfie (1918)	Yorke & Macfie (1920)
Cyathostominae																	
Cyathostomum alveatum							+	+			+			+			
Cyathostomum montgomeryi	+										+			+			
Cyathostomum tetracanthum							+				+			+			
*Cylicocyclus adersi**	+										+			+			
Cylicocyclus auriculatus							+	+			+			+			
Cylicocyclus triramosus							+				+			+			+
Cylicodontophorus reineckei													+				
Cylicodontophorus schuermanni									+								
Cylicostephanus bidentatus			+				+										
Cylicostephanus calicatus				+			+	+			+			+			
Cylicostephanus longiconus												+					
Cylicostephanus minutus	+						+									+	
Cylindropharynx spp.		+			+	+								+			+
Strongylinae**																	
Craterostomum acuticaudatum				+			+							+			
Triodontophorus serratus							+	+		+				+			
Habronematidae***																	
Draschia megastoma														+			
Habronema majus														+			
Habronema zebrae														+			
Atractidae																	
Crossocephalus viviparus					+									+			
Probstmayria vivipara							+							+			
Oxyuridae																	
Oxyuris equi							+										
Onchocercidae																	
Setaria equina															+		

* Described by Boulenger (1920a)

** In addition, 2 new *Triodontophorus* spp. were identified and in this manuscript will be referred to as *Triodontophorus* n. sp. (A) and *Triodontophorus* n. sp. (B)

*** Likewise, 2 new *Habronema* spp. which were recovered will be referred to as *Habronema* n. sp. (A) and *Habronema* n. sp. (B)

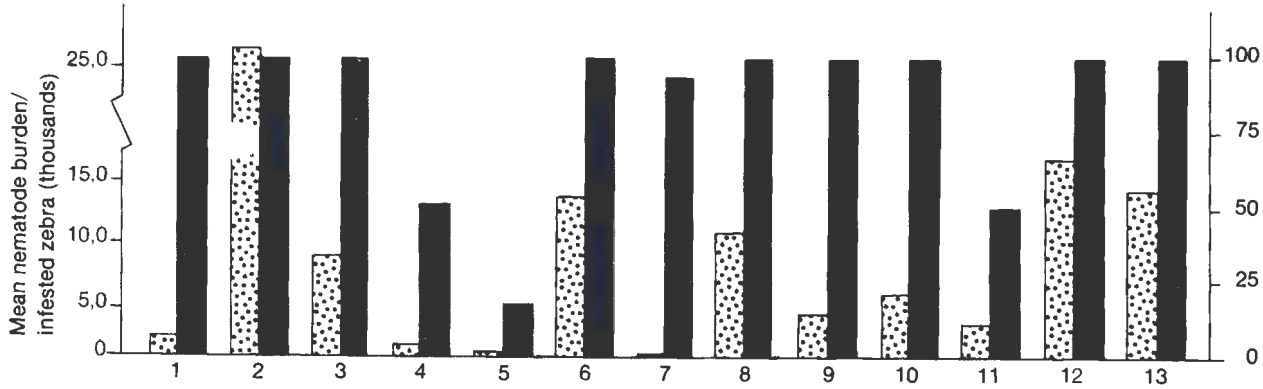

FIG. 6 Mean nematode burdens (□) and prevalence (■) of Burchell's zebras infested with 13 species of cyathostomes, Etosha, 1982. 1. *Cyathostomum alveatum*, 2. *Cyathostomum montgomeryi*, 3. *Cyathostomum tetracanthum*, 4. *Cylicocyclus adersi*, 5. *Cylicocyclus auriculatus*, 6. *Cylicocyclus triramosus*, 7. *Cylicodontophorus reineckei*, 8. *Cylicodontophorus schuermanni*, 9. *Cylicostephanus bidentatus*, 10. *Cylicostephanus calicatus*, 11. *Cylicostephanus longiconus*, 12. *Cylicostephanus minutus*, 13. *Cylindropharynx* sp. (? *intermedia*)

DISCUSSION

This is the first report of infestation of mountain zebras by *Cyathostomum alveatum, Cyathostomum montgomeryi, Cylicostephanus bidentatus* and *Draschia megastoma*. *Triodontophorus* n. sp. (A) was recovered from the Burchell's zebras, but not from mountain zebras at Etosha. This is the first report of *Cylicostephanus longiconus* infesting Burchell's zebras. This species had previously been recovered only from mountain zebras (Scialdo-Krecek, 1983 b; Scialdo-Krecek *et al.* 1983).

Cyathostomes most abundant in Etosha's Burchell's zebras were: *Cyathostomum montgomeryi* (7 120–67 042), *Cylicocyclus triramosus* (11–34 540), *Cylicostephanus* minutus (4 698—40 019) and *Cylindropharynx* sp. (? *intermedia*) (3 591–40 018). Atractids with the highest burdens were: *Crossocephalus viviparus*

TABLE 2 Faecal nematode egg counts and total nematode burdens of Strongylidae, Oxyuridae and Onchocercidae recovered from Burchell's zebras (B), Otjovasandu and Okaukuejo, Etosha, March 1982—November 1982 (*B_1/B_6/B_9—Okaukuejo area)

Zebra No.	*B_1	B_2	B_3	B_4	B_5	*B_6	B_7	B_8	*B_9			
Age (yr)/Sex	6/M	11/M	6/M	4½/M	5/M	6½/F	8½/F	8½/M	19/M			
Date killed/Season**	4/3/82/Su	3/3/82/Su	3/3/82/Su	13/7/82/W	13/7/82/W	14/7/82/W	23/11/82/S	23/11/82/S	24/11/82/S			
Eggs per gram of faeces	N.D.(1)	N.D.	N.D.	2 150	1 850	1 400	2 150	4 950	N.D.	Total	Zebras positive	Range
Cyathostominae												
L_4 Cyathostominae	329	3	87	7 595	8 906	9 019	1 118	1 193	1 240	29 490	9	3–9019
Cyathostomum alveatum	360	100	136	1 344	215	56	246	449	3 352	6 258	9	56–3352
Cyathostomum montgomeryi	22 937	19 791	11 179	20 903	16 625	46 012	7 120	17 163	67 042	228 772	9	7120–67042
Cyathostomomum tetracanthum	21 322	4 774	5 556	1 883	8 510	6 918	4 124	5 245	14 153	72 485	9	1883–21322
Cylicocyclus adersi	100	0	0	2	420	1 300	0	800	0	2 622	5	2–1300
Cylicocyclus auriculatus	0	0	0	0	1 140	1 318	0	0	0	2 458	2	—
Cylicocyclus triramosus	11 718	11 580	8 327	12 580	34 540	26 918	7 867	14 791	11	128 332	9	11–34540
Cylicodontophorus reineckei	50	0	4	60	40	2	12	487	11	666	8	2–487
Cylicodontophorus schuermanni	733	300	300	12 686	46 027	36	8 705	16 109	14 210	99 106	9	36–46027
Cylicostephanus bidentatus	5 979	1 212	5 150	151	2 085	1 167	12 084	3 920	8 071	39 819	9	151–12084
Cylicostephanus calicatus	2 288	5 330	2 800	7 458	10 525	6 064	2 789	9 214	2 141	48 609	9	2141–10525
Cylicostephanus longiconus	2 805	0	0	0	0	2 600	2 512	1 720	8 680	18 317	5	1720–8680
Cylicostephanus minutus	5 787	8 198	4 698	6 640	30 865	31 323	7 361	8 307	40 019	143 198	9	4698–40019
Cylindropharynx sp. (? *intermedia*)	30 209	4 842	15 100	5 031	13 221	3 591	21 508	14 110	40 018	147 630	9	3591–40018
Strongylinae												
Craterostomum acuticaudatum	937	1 350	1 450	372	2 015	7 140	1 454	860	11 751	27 329	9	372–11751
Triodontophorus n. sp. (A)	0	950	0	16	100	0	0	0	0	1 066	3	16–950
Triodontophorus n. sp. (B)	0	0	0	0	0	0	0	0	0	0	0	—
Triodontophorus serratus	0	0	0	0	0	0	0	0	0	0	0	—
Oxyuridae												
Oxyuris equi L_4	1	450	0	0	647	0	0	0	9	1 107	4	1–647
Oxyuris equi Adult	3	0	0	7	27	0	0	0	0	37	3	3–27
Onchocercidae												
Setaria equina	0	55	17	0	0	0	6	45	9	132	5	6–55

** Su = Summer, W = Winter, S = Spring

(1) N.D. = not determined

TABLE 3 Faecal nematode egg counts and total nematode burdens of Strongylidae, Oxyuridae and Onchocercidae recovered from mountain zebras (M), Otjovasandu, Etosha, March 1982—November 1982

Zebra No.	M1	M2	M3	M4	M5	M6			
Age (yr)/Sex	4½/M	4½/F	12/M	3½/F	13/M	13/F			
Date killed/Season*	2/3/82/Su	2/3/82/Su	12/7/82/W	12/7/82/W	22/11/82/S	22/11/82/S	Total	Zebras positive	Range
Eggs per gram of faeces	N.D.(1)	N.D.(1)	1 000	850	1 750	1 150			
Cyathostominae									
L_4 Cyathostominae	15	52	15 065	5 965	11 316	16 260	48 673	6	15–16 260
Cyathostomum alveatum	886	222	221	201	1 331	498	3 359	6	201–1 331
Cyathostomum montgomeryi	0	1 020	1	460	10	51	1 542	5	1–1 020
Cyathostomomum tetracanthum	61	7 403	5 809	1 084	3 793	3 045	21 195	6	61–7 403
Cylicocyclus adersi	55	210	50	0	1 716	932	2 963	5	50–1 716
Cylicocyclus auriculatus	162	4 560	0	5	1 050	558	6 335	5	5–4 560
Cylicocyclus triramosus	54	3 281	19 782	1 399	1 423	1 791	27 730	6	54–19 782
Cylicodontophorus reineckei	0	0	0	0	0	0	0	0	—
Cylicodontophorus schuermanni	100	100	2 509	60	1	2 263	5 033	6	1–2 509
Cylicostephanus bidentatus	0	0	100	0	5	0	105	2	—
Cylicostephanus calicatus	18	2 050	1 261	320	569	803	5 021	6	18–2 050
Cylicostephanus longiconus	0	2	950	155	627	280	2 014	5	2–950
Cylicostephanus minutus	555	4 073	1 894	2 010	10 322	12 396	31 250	6	555–12 396
Cylindropharynx sp. (? *intermedia*)	2 617	4 887	317	3	3 595	5 325	16 744	6	3–5 325
Strongylinae									
Craterostomum acuticaudatum	0	1	3	73	50	0	127	4	1–73
Triodontophorus n. sp. (A)	0	0	0	0	0	0	0	0	—
Triodontophorus n. sp. (B)	209	1 865	1 206	58	95	219	3 652	6	58–1 865
Triodontophorus serratus	34	9	5	15	0	0	63	4	5–34
Oxyuridae									
Oxyuris equi L_4	1	150	0	7	0	0	158	3	1–150
Oxyuris equi adults	0	0	0	0	0	0	0	0	—
Onchocercidae									
Setaria equina	71	34	141	1	133	104	484	6	1–141

* Su = Summer, W = Winter, S = Spring
(1) N.D. = Not determined

TABLE 4 Total nematode burdens of Atractidae and Habronematidae recovered from Burchell's sebras (B), Otjovasandu and Okaukuejo, Etosha, March–November 1982 (*B_1/B_6/B_9—Okaukuejo area)

Zebra No.	*B_1	B_2	B_3	B_4	B_5	*B_6	B_7	B_8	*B_9	Total	Zebras Positive	Range
Date Killed	3/82	3/82	3/82	7/82	7/82	7/82	11/82	11/82	11/82			
Atractidae												
Crossocephalus viviparus	23 400**	282 763**	112 161**	8 106**	314 250**	20	5 045 212**	2 767 430**	60**	8 553 410	9	20–5 045 212
Probstmayria vivipara	171 540	19 050	5 140	462 180	1 389 630	677 400	135 400	3 256 184	3 801 300	9 917 824	9	5 140–3 801 300
Habronematidae												
Draschia megastoma	3	788	32	43	103	64	376	409	402	2 220	9	3–788
Habronema n. sp. (A)	16	3	0	4	0	0	42	0	0	65	4	3–42
Habronema majus	1	2	0	52	0	7	22	4	43	131	7	1–52
**Division of *C. viviparus* according to sex and stages: Y = Young	2 600	16 203	4 170	560	18 440	0	707 141	191 508	0	—	—	—
F = Female	12 690	185 899	47 451	3 983	226 580	20	3 338 330	1 082 268	60	—	—	—
FP = Female bearing young	1 860	9 200	5 810	130	17 210	0	2 517	67 467	0	—	—	—
M = Male	6 250	71 461	54 730	3 433	52 020	0	997 224	1 426 187	0	—	—	—

TABLE 5 Total nematode burdens of Atractidae and Habronematidae recovered from mountain zebras (M), Otjovasandu, Etosha, March–November 1982

Zebra No.	M1	M2	M3	M4	M5	M6	Total	Zebras positive	Range
Date Killed	3/82	3/82	7/82	7/82	11/82	11/82			
Atractidae									
Crossocephalus viviparus	0	200*	0	510*	400*	40	1 150	4	40–510
Probstmayria vivipara	0	0	212 410	419 800	10	10	632 230	4	10–419 800
Habronematidae									
Draschia megastoma	20	0	75	8	157	430	690	5	8–430
Habronema n. sp. (A)	0	0	0	21	0	0	21	1	—
Habronema majus	652	178	296	0	150	180	1 456	5	150–652
*Division of *C. viviparus* according to sex and stages Y = Young	0	0	0	10	0	0	—	—	—
F = Female	0	0	0	500	300	40	—	—	—
FP = Female bearing young	0	0	0	0	0	0	—	—	—
M = Male	0	200	0	0	100	0	—	—	—

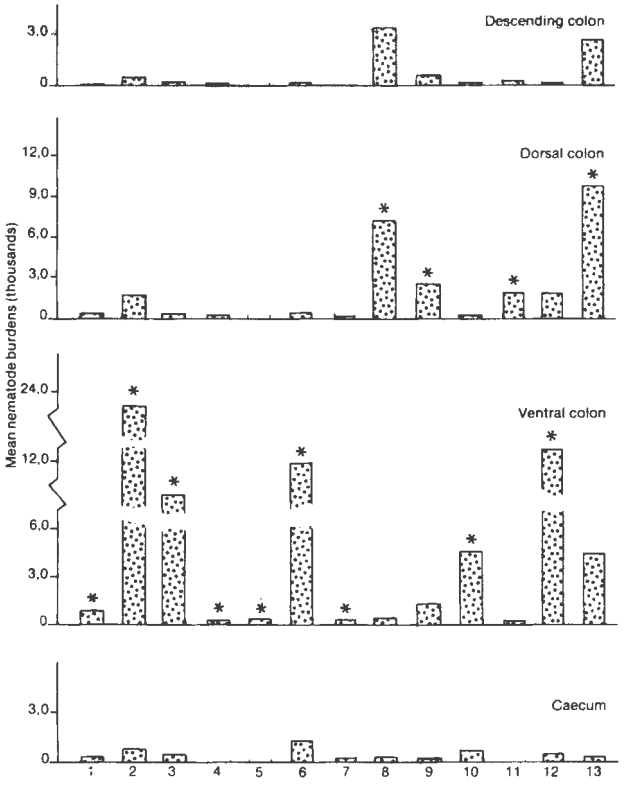

FIG. 7 The distribution of cyathostomes in the intestinal tract of Burchell's zebras, Etosha, 1982. * = preferred site. 1. *Cyathostomum alveatum*, 2. *Cyathostomum montgomeryi*, 3. *Cyathostomum tetracanthum*, 4. *Cylicocyclus adersi*, 5. *Cylicocyclus auriculatus*, 6. *Cylicocyclus triramosus*, 7. *Cylicodontophorus reineckei*, 8. *Cylicodontophorus schuermanni*, 9. *Cylicostephanus bidentatus*, 10. *Cylicostephanus calicatus*, 11. *Cylicostephanus longiconus*, 12. *Cylicostephanus minutus*, 13. *Cylindropharynx* sp. (? *intermedia*)

(20–5 045 212) and *Probstmayria vivipara* (5 140–3 801 300). Three of the above cyathostome species *Cylicocyclus triramosus* (54–19 782), *Cylicostephanus minutus* (555–12 396) and *Cylindropharynx* sp. (? *intermedia*) (3–5 325), were also abundant in Etosha's mountain zebras.

That *Cylicostephanus calicatus* and *Cylicostephanus minutus* were recovered from the ventral colon confirms Theiler's (1923) earlier findings for zebras and Hasslinger's (1963) for horses. The presence of *Poteriostomum ratzii* in the dorsal colon of the zebra is also in agreement with the findings of Ogbourne (1976) for domestic equids. However, Theiler (1923) recovered *Poteriostomum ratzii* from both the ventral and dorsal colon in zebras.

Peak numbers of L_4 cyathostomes in the gut wall occurrred in early winter in Burchell's zebras in Etosha and in both early winter and spring in the Etosha mountain zebras. This follows the pattern of previous surveys (Scialdo *et al.*, 1982; Scialdo-Krecek *et al.*, 1983) and corroborates Ogbourne's (1971) and Poynter's (1954) findings in which L_4 cyathostomes were thought to overwinter in the gut wall. In addition, in mountain zebras more L_4 were present in the wall of the small intestine than in either the caecal or colonic wall.

Apart from *Cylicocyclus adersi* (Boulenger, 1920), *Cylicocyclus auriculatus*, *Triodontophorus* n. sp. (B) and *Triodontophorus serratus*, all nematode species were present in higher infestations in Burchell's zebras. Since there were greater numbers of 4th stages (L_4) and fewer numbers of 5th and adult stages in mountain zebras, it appears that the larval stages of the cyathostomes may be overwintering in greater numbers in the gut wall and not developing further. Hence, lower total burdens of the 5th and adult stages occur in the lumen of the gut of this host. It is postulated, therefore, that these 4 nematode species have adapted in the mountain zebra to overwinter longer than in the Burchell's zebra, that is, these immature nematodes (L_4) encyst in nodules in the intestinal wall for a prolonged period. This adaptation thus provides an extension (or interruption) of the nematode's life cycle.

Whereas both host species depend on water the Burchell's zebra is more water-dependent (Smithers, 1983). Furthermore, Smithers states that it is a savanna species, partial to open areas of woodland, open scrub and grassland where water is available. Hence, this zebra is never more than 10–12 km from water. According to Smithers (1983), the Hartmann's mountain zebras in contrast generally inhabit mountains, deserts and open sandy plains (Iona National Park, south-western Angola) and are known to travel 100 km to seek water. The same author states that this host has evolved a behavioural adaptation to dig underground with its hooves for water if surface water is non-existent. It is possible that the cyathostome species, infesting mountain zebras which have adapted to a more arid environment than Burchell's zebras, have adjusted their strategy for survival. Perhaps seasonal variations applying to their host trigger these nematodes to invade the small and large intestinal walls in the "dry" season, emerge from their larval stages in spring and develop to adults when they receive and respond to the appropriate cues.

Parasitic nematodes in their normal definitive host (the host in which parasites reach maturity and reproduce sexually) do not always reach adulthood within a developmental period of characteristic length, and prolonged interruption of the life cycle is a frequent alternative

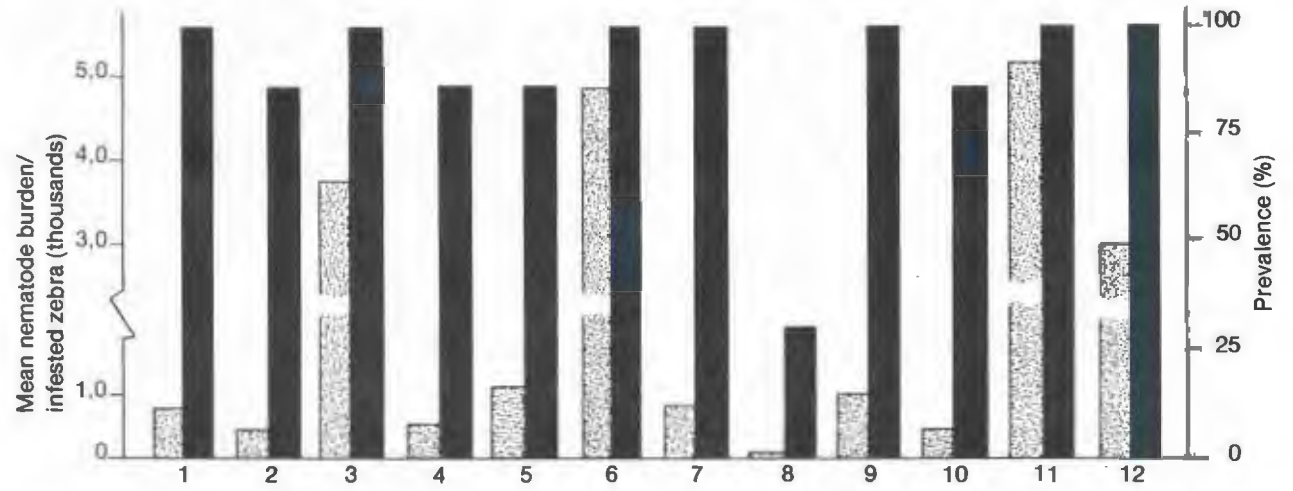

FIG. 8 Mean nematode burdens (□) and prevalence (■) of mountain zebras infested with 12 species of cyathostomes, Etosha, 1982. 1. *Cyathostomum alveatum*, 2. *Cyathostomum montgomeryi*, 3. *Cyathostomum tetracanthum*, 4. *Cylicocyclus adersi*, 5. *Cylicocyclus auriculatus*, 6. *Cylicocyclus triramosus*, 7. *Cylicodontophorus schuermanni*, 8. *Cylicostephanus bidentatus*, 9. *Cylicostephanus calicatus*, 10. *Cylicostephanus longiconus*, 11. *Cylicostephanus minutus*, 12 *Cylindropharynx* sp. (? *intermedia*)

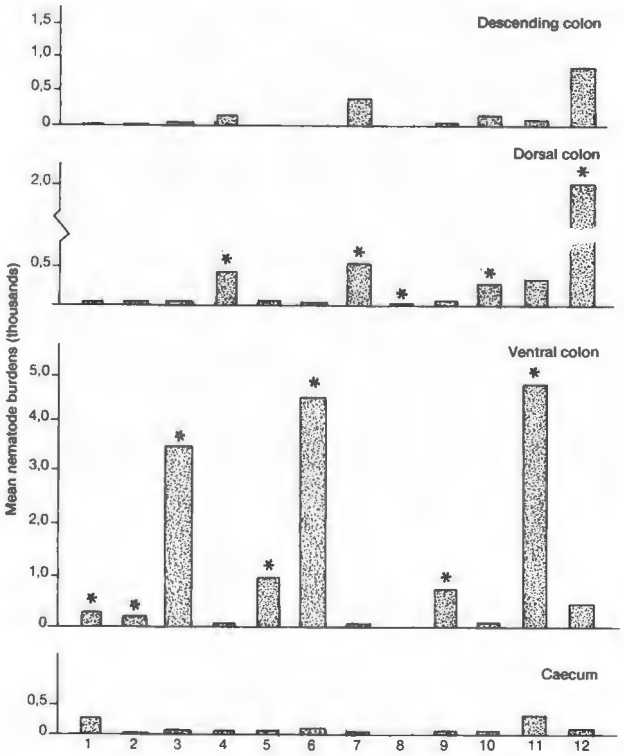

Fig. 9 The distribution of cyathostomes in the intestinal tract of mountain zebras, Etosha, 1982. *=preferred site. 1. *Cyathostomum alveatum*, 2. *Cyathostomum montgomeryi*, 3. *Cyathostomum tetracanthum*, 4. *Cylicocyclus adersi*, 5. *Cylicocyclus auriculatus*, 6. *Cylicocyclus triramosus*. 7. *Cylicodontophorus schuermanni*. 8. *Cylicostephanus bidentatus*. 9. *Cylicostephanus calicatus*, 10. *Cylicostephanus longiconus*, 11. *Cylicostephanus minutus*, 12. *Cylindropharynx* sp. (? *intermedia*)

(Schad, 1977). According to Horak (1980) a number of factors or cues have been proposed which may explain this interruption or arrested (inhibited) development. It should be emphasized that thus far the most comprehensive studies investigating arrested development have been with parasites in the digestive tract of ruminants. Such factors fall into 3 categories:

1. External environmental factors acting on the free-living stages (e.g. aging of larvae, chilling and reduction in photo-period).
2. Host factors, which determine the host's suitability for further development, and which, when adverse conditions may load to arrest (e.g. host's diet, age of the host, acquired resistance, endocrine changes in the host and environmental factors acting on the host) and
3. Parasite-related factors which are either genetic or density-dependent (e.g. number of larvae dosed or presence of adult worms).

Horak (1980), however, proposed a different approach to the subject of arrested development. He included 2 types of inhibition, non-specific and seasonal arrested development. The latter is defined as occurring annually during the same season and is generally dependent upon the nematodes affected being adapted to a particular environment (Horak, 1980; 1983). He suggested that these nematodes were susceptible to 1 or several seasonal external environmental stimuli acting upon the infective larvae and resulting in arrest in a later stage of development.

We are in agreement with Horak (1980, 1983), as the arrested larval development in the zebras is seasonal. The numbers of larvae and adult nematodes recovered from the 2 zebra host species differ, and therefore each responds to the cues that result in the arrested development of L_4 cyathostomes.

ACKNOWLEDGEMENTS

The authors wish to thank the University of Pretoria for financial assistance; the late Dr J. M. Hofmeyr for his co-operation and his staff for their assistance throughout this study; the Department of Agriculture and Nature Conservation of South West Africa/Namibia; Drs An de Ruyck, Robin Kirkpatrick, Martin Schulman, Mr I. L. de Villiers, Dr H. C. Biggs of the Directorate of Veterinary Services, Mrs Dagmar Rautsch and Mr N. Anthonissen of the Central Veterinary Laboratory, Mr Jan le Roux, Mr. T. E. Krecek and Mmes Daleen Lombard and Bonny Roper for technical assistance.

REFERENCES

BERRY, H. H., 1980. Behavioural and eco-physiological studies on blue wildebeest *(Connochaetes taurinus)* at the Etosha National Park. Ph.D. thesis, University of Cape Town.

BOULENGER, C. L., 1920 a. Sclerostomes of the donkey in Zanzibar and East Africa. *Parasitology*, 12, 27–32.

BOULENGER, C. L., 1920 b. On some nematode parasites of the zebra. *Parasitology*, 12, 98–107.

CRAM, ELOISE B., 1924. A new nematode, *Cylindropharynx ornata*, from the zebra, with keys to related nematode parasites of the Equidae. *Journal of Agricultural Research*, 28, 661–672.

GIESS, W., 1971. A preliminary vegetation map of South West Africa. *Dinteria*, 4, 5–14.

HASSLINGER, M. A., 1963. Untersuchungen an Schlachtpferden über Vorkommen und Sitz Verschiedener kleiner Strongyliden-Arten. Inaugural Dissertation, Freie Universität, Berlin.

HORAK, I. G., 1980. The incidence of helminths in pigs, sheep, cattle, impala and blesbok in the Transvaal. Ph.D. thesis, University of Natal.

HORAK, I. G., 1983. Helminth, arthropod and protozoan parasites of mammals in African savannas. *In:* BOURLIÈRE, F. (ed.). Tropical savannas. 563–581. Amsterdam: Elsevier Scientific Publishing company.

IHLE, J. E. W., 1925. Verzeichnis der Cylicostomum-Arten der Equiden, mit Bemerkungen über einzelne Spezies. *Zentralblatt für Bakteriologie, Parasitenkunde und Infektions-krankheiten,* 95, 227–236.

KOTLÁN, S., 1919. Beiträge zur Helminthologie ungarns. 1. Neue Sclerostomiden aus dem Pferd. *Zentralblatt für Bakteriologie, Parasitenkunde und Infektionskrankheiten,* 83, 557–560.

LEIPER, R. T., 1911. Some new parasitic nematodes from Tropical Africa. *Proceedings of the Zoological Society of London,* 36, 549–555.

LE, ROUX, P. L., 1932. List of helminths collected from mammals and birds in the Mazabuka area, Northern Rhodesia. *Report of the Department of Animal Health of Northern Rhodesia,* Appendix B, 31–34.

LE, VAN HOA, 1962. Nematodes Parasites de Mammiferes, Reptiles et Amphibiens du Congo. Phasmidiens. *Parc National De l'Upemba—Mission G. F. de Witte,* 65, 3–58.

LICHTENFELS, J. R., 1975. Helminths of domestic equids. Illustrated keys to genera and species with emphasis on North American forms. *Proceedings of the Helminthological Society of Washington,* 42, Special issue p. 92.

LOOSS, A., 1900. Notizen zur Helminthologie Egyptens. III. Die Sclerostomen der Pferde und Esel in Egypten. *Zentralblatt für Bakteriologie, Parasitenkunde und Infektionskrankheiten,* 27, 184–192.

MALAN, F. S., REINECKE, R. K. & SCIALDO, ROSINA C., 1981 a. Recovery of helminths post-mortem from equines. I. Parasites in arteries, subperitoneum, liver and lungs. *Onderstepoort Journal of Veterinary Research,* 48, 141–143.

MALAN, F. S., REINECKE, R. K. & SCIALDO, ROSINA C., 1981 b. Recovery of helminths post-mortem from equines. II. Helminths and larvae of *Gasterophilus* in the gastro-intestinal tract and oestrids from the sinuses. *Onderstepoort Journal of Veterinary Research,* 48, 145–147.

MÖNNIG, H. O., 1928. Checklist of the worm parasites of domesticated animals in South Africa. *Report of the Director of Veterinary Education and Research, Union of South Africa,* 13/14, 801–837.

OGBOURNE, C. P., 1971. Variations in the fecundity of strongylid worms of the horse. *Parasitology,* 63, 289–298.

OGBOURNE, C. P., 1976. The prevalence, relative abundance and site distribution of nematodes of the subfamily Cyathostominae in horses killed in Britain. *Journal of Helminthology,* 50, 203–214.

ORTLEPP, R. J., 1962. *Trichonema (Cylicodontophorus) schürmanni* sp. nov. from a zebra *(Equus burchelli* Gray, 1924). *Onderstepoort Journal of Veterinary Research,* 29, 169–172.

POPOVA, T. I., 1955. Strongyloids of animals and man. Trichonematidae. K. I. SKRJABIN (ed.). Essentials of Nematology. Vol. 5. Jerusalem: Israel Program for Scientific Translations, 1964.

POPOVA, T. I., 1958. Strongyloids of animals and man. Trichonematidae. K. I. SKRJABIN (ed.). Essentials of Nematology. Vol. 7. Jerusalem: Israel Program for Scientific Translations, 1965.

POYNTER, D., 1954. Seasonal fluctuations in the number of strongyle eggs passed by horses. *Veterinary Record,* 66, 74–78.

SCHAD, G. A., 1977. The role of arrested development in the regulation of nematode populations. *In:* EACH, G. W. (ed.) Regulation of parasite populations, 111–167. New York: Academic Press.

SCIALDO, ROSINA, C., REINECKE, R. K. & DE, VOS,, V., 1982. Seasonal incidence of helminths in the Burchell's zebra. *Onderstepoort Journal of Veterinary Research,* 49, 127–130.

SCIALDO-KRECEK, ROSINA C., 1983 a. Studies on the parasites of zebras. I. Nematodes of the Burchell's zebra in the Kruger National Park. *Onderstepoort Journal of Veterinary Research,* 50, 111–114.

SCIALDO-KRECEK, ROSINA C., 1983 b. Studies on the parasites of zebras. II. *Cylicostephanus longiconus* n. sp. (Nematoda: Strongylidae) from the mountain zebra, *Equus zebra hartmannae* (Matschie, 1898). *Onderstepoort Journal of Veterinary Research,* 50, 169–172.

SCIALDO-KRECEK, ROSINA C., REINECKE, R. K. & BIGGS, H. C., 1983. Studies on the parasites of zebras. III. Nematodes of the mountain zebra from the farm "Kelpie" and the Namib-Naukluft Park, South West Africa/Namibia. *Onderstepoort Journal of Veterinary Research,* 50, 283–290.

SCIALDO-KRECEK, ROSINA C. & MALAN, F. S., 1984. Studies on the parasites of zebras. IV. *Cylicodontophorus reineckei* n. sp. (Nematoda: Strongylidae) from the Burchell's zebra, *Equus burchelli antiquorum* H. Smith, 1841 and the mountain zebra, *Equus zebra hartmannae* (Matschie, 1898). *Onderstepoort Journal of Veterinary Research,* 51, 257–262.

SMITHERS, R. H. N., 1983. The mammals of the southern African subregion. Pretoria: University of Pretoria.

THEILER,GERTRUD, 1923. The strongylids and other nematodes parasitic in the intestinal tract of South African equines. *Report of the Director of Veterinary Education and Research, Union of South Africa,* 9/10, 601–773.

YEH, LIANG-SHENG, 1959. A revision of the nematode genus *Setaria* Viborg, 1795, its host-parasite relationship, speciation and evolution. *Journal of Helminthology,* 33, 1–98.

YORKE, W. & MACFIE, J. W. S., 1918. Strongylidae in horses. II. *Cylicostomum minutum* sp. n. *Annals of Tropical Medicine & Parasitology,* 11, 405–409.

YORKE, W. & MACFIE, J. W. S., 1920. Strongylidae in horses. XII. *Cylindropharynx rhodesiensis* sp. n. *Annals of Tropical Medicine & Parasitology,* 15, 169–174.

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