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PARASITES OF DOMESTIC AND WILD ANIMALS IN SOUTH AFRICA. XVI. HELMINTH AND ARTHROPOD PARASITES OF BLUE AND BLACK WILDEBEEST *(CONNOCHAETES TAURINUS* AND *CONNOCHAETES GNOU)*

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ABSTRACT

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Fifty-five blue wildebeest *(Connochaetes taurinus)* were shot for parasite recovery at approximately monthly intervals during a period of 13 months in the Kruger National Park. Thirteen nematode species, 4 cestode species, 1 trematode, the larvae of 5 oestrid flies, 3 lice species, 7 ixodid tick species, 1 mite species and the nymphae of a pentastomid were recovered. The seasonal prevalence of 8 nematodes, 2 cestodes, the larvae of 4 oestrid flies, 2 lice and 4 ixodid tick species was determined.

The endo- and ectoparasite burdens of 7 black wildebeest *(Connochaetes gnou)* shot in the Golden Gate Highlands Park in the Orange Free State and 3 shot in the Rietvlei Reserve in the Transvaal were determined. These animals harboured 4 nematode species, 1 cestode, the larvae of 5 oestrid fly species, 2 lice species, 4 ixodid tick species and a mite species.

INTRODUCTION

A progressive decline since 1970 in the numbers of blue wildebeest *(Connochaetes taurinus)* in the Kruger National Park, situated in the eastern Transvaal Lowveld, prompted an investigation to determine whether infestations with helminth and arthropod parasites were responsible. Previous investigations in blesbok *(Damaliscus dorcas phillipsi)*, impala *(Aepyceros melampus)* and greater kudu *(Tragelaphus strepsiceros)* had demonstrated that free-ranging antelope can harbour large burdens of several species of parasites and that these burdens are subject to considerable seasonal fluctuations (Horak & Butt, 1977; Horak, 1978a,b; 1982; Knight & Rechav, 1978). Consequently it was decided that the best method of determining what parasites were present, and whether their numbers ever reached pathogenic levels, was to do complete parasite counts on blue wildebeest at monthly intervals over a period of 13 months.

Black wildebeest bulls *(Connochaetes gnou)* are culled occasionally, as a means of population control, in the Golden Gate Highlands Park in the eastern Orange Free State and in the Rietvlei Nature Reserve in the central Transvaal. This presented the opportunity to determine the parasitic helminth and arthropod fauna of these animals.

MATERIALS AND METHODS

Blue wildebeest

The survey was conducted in the southern region of the Kruger National Park between Satara (24° 24′ S, 31° 47′ E; Alt. 275 m) and Lower Sabie (25° 07′ S, 31° 55′ E; Alt. 180 m), a region comprising Arid Lowveld and Lowveld (Acocks, 1975). Rainfall and atmospheric temperature were measured at Skukuza (24° 58′ S, 31° 36′ E; Alt. 262 m), situated to the west of the study area within the park.

Each month from November 1977 to November 1978 an attempt was made to shoot 2 wildebeest calves from the most recent calf-crop as well as 2 animals from the previous crop. As the majority of wildebeest in the park are born during December this culling procedure meant that the animals examined during the course of the 13 month survey ranged from 1–24 months in age.

Because the survey started in November 1977 and ended during November 1978 it also meant that 1–11-month-old animals were shot from January–November 1978, 11–23-month-old animals from November 1977–November 1978 and 23- and 24-month-old animals during November and December 1977. Occasionally older animals were also shot, and once an additional 2 calves badly affected by sarcoptic mange were culled. A total of 55 animals were examined.

Immediately after they had been shot, the animals were exsanguinated and eviscerated. The viscera were placed in plastic bags, as were the unskinned heads and unskinned legs below the hock and knee joints. These bags and the carcasses were transported to the laboratory at Skukuza. There the skins were removed from the upper legs, bodies and necks and from the heads and placed in plastic bags. The skin of the lower legs was left intact.

The gastro-intestinal tracts, livers and lungs were processed for helminth recovery as described by Horak, Meltzer & De Vos (1982), but the mucosae of the abomasa, small intestine and large intestines were digested separately with pepsin and HC1. Faeces were collected for faecal worm egg counts and coccidial oocyst counts.

The nasal passages, sinuses and hearts were processed for the recovery of larvae of oestrid flies as described by Horak & Butt (1977). In addition the dura from half of the cranial cavity was stripped and placed in 70% alcohol and 10% formalin for later examination. The mature oestrid larvae were collected and allowed to pupate in vermiculite in gauze-stoppered bottles kept at Skukuza in a room with 3 walls consisting largely of gauze screens and a 4th solid wall. The bottles were inspected daily and the dates on which the flies hatched were noted.

The lower legs, skins of the heads and skins of the upper legs, bodies and necks of the first 4 animals were processed for ectoparasite recovery as desbribed by Horak (1982). The ticks and lice recovered from these animals are not included in the tables or graphs reflecting ectoparasite burdens because the recovery method was inferior to that employed thereafter. In the case of the remaining animals the lower legs (feet to the knee or hock joints) with skin intact; the skin of the head; and the skin of the upper legs, body and neck, were placed separately in deep plastic trays containing a tick-detaching agent* for approximately 10 minutes. Thereafter the various parts were replaced in the plastic bags from which they had been taken and these were tightly closed. The fluid in which they had been immersed was sieved through sieves with 150 μm apertures and the contents of the sieves were collected and preserved with formalin. The following morning the lower legs; skins of the heads; skins of the upper legs, bodies and necks and the plastic bags in which they had been held were thor-

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oughly washed and the washings poured through sieves with 150 µm apertures. The various parts were then scrubbed several times with brushes with 20 mm long steel bristles and washed. The scrubbings and washings were poured through sieves with 150 µm apertures and the contents of the sieves added to the material already collected.

Worms were counted by examining the lung washings, liver filtrates and digests of the abomasum, small intestine and large intestine *in toto,* and 2 1/50th aliquots of the contents of the latter 3 organs under a stereoscopic microscope. The residue of the small and large intestinal contents was examined macroscopically for adult *Gaigeria, Agriostomum* and *Oesophagostomum* and for cestodes. Worms were identified under the stereoscopic or standard microscope.

All oestrid fly larvae were counted and identified under the stereoscopic microscope. The skin scrapings were examined *in toto* under the stereoscopic microscope and all the lice and nymphal and adult ticks counted and identified. When less than 200 larval ticks were present in a sample, all were counted and identified; if more were found all were counted and at least 200 identified.

Comment: The various monthly age groups of blue wildebeest were not shot consecutively as the survey commenced in November 1977 when the youngest wildebeest were already 11 months of age and those a year older were 23 months of age. Thus it was only during January 1978, when the survey had already been in progress for 2 months, that 1-month- and 13-month-old wildebeest were shot. Nevertheless the graphic representations of their parasite burdens have been drawn as though they were shot consecutively from 1–24 months of age. A distinction is made in the graphs, however, between the animals shot during 1977 and those shot during 1978.

Black wildebeest

During March 1979 4 bulls and during December 1979 3 bulls were shot in the Golden Gate Highlands Park (28° 31′ S, 28° 37′ E; Alt. 1 798–2 731 m) in the eastern Orange Free State. This park is 4 792 ha in extent and in addition to black wildebeest contains blesbok, eland, oribi, red hartebeest, springbok and Burchell's zebra. It is situated in a region classified as Highland Sourveld (Acocks, 1975).

During July and August 1981, 3 black wildebeest bulls were shot in the Rietvlei Nature Reserve (25° 53′ S, 28° 17′ E; Alt. ± 1 500 m) to the south-east of Pretoria in the central Transvaal. This reserve, which is approximately 3 000 ha in extent, lies within a region classified as Bankenveld (Acocks, 1975) and, in addition to black wildebeest, contains blesbok, red hartebeest, eland, springbok, duiker, steenbok, oribi and Burchell's zebra.

The black wildebeest shot in these parks were processed in the same way as the latter group of blue wildebeest for the recovery of endo- and ectoparasites.

RESULTS

Blue wildebeest

Coccidia

The mean faecal oocyst counts of the wildebeest, ranked by age, are graphically illustrated in Fig. 1. These counts were generally considerably higher in animals 1–7 months of age than in older animals.

Helminths

The helminth parasites recovered, their abundance and prevalence are summarized in Table 1.

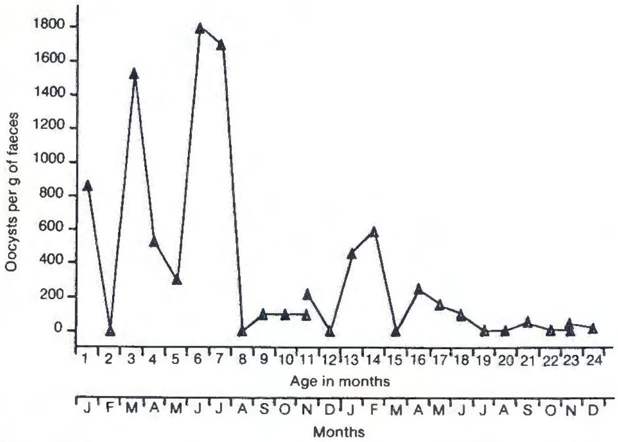

FIG. 1 The coccidial oocyst counts of 1–24-month-old blue wildebeest in the Kruger National Park

Thirteen species of nematodes, 4 cestodes and the cysticerci of *Taenia regis* and 1 trematode species were recovered. *Haemonchus bedfordi* was the most prevalent of the nematodes recovered and *Cooperia connochaeti* the most abundant. *Moniezia benedeni* was the most abundant of the cestodes and *Avitellina* sp. the most prevalent.

The mean nematode egg counts and the mean worm burdens of the wildebeest ranked by age are graphically illustrated in Fig. 2–4.

Faecal nematode egg counts exhibited autumn and spring peaks, those in the 1–12-month-old animals being generally higher than those in the 13–24-month-old antelope (Fig. 2).

Dictyocaulus viviparus infestation was first encountered in a 5-month-old animal and although worm burdens were small and varied considerably, the older animals tended to harbour more worms than those a year younger (Fig. 3A).

With the exception of a 6-month-old animal which had broken its leg and harboured 575 worms; a 15-month-old animal which had 1 worm; and a 16-month-old animal which has 25 worms, *Strongyloides* sp. infestations were confined to animals 1–5 months of age. The highest burdens were encountered in the 1-month-old animals (Fig. 3A).

H. bedfordi reached peak numbers during April and October in the 1–12-month-old animals and only during April in the older animals (Fig. 3B). *Trichostrongylus thomasi* followed a similar pattern to *H. bedfordi* but its peaks were always later than those of the latter worm, namely, June and November in the younger animals and only June in the older ones (Fig. 3C).

C. connochaeti also followed a fairly similar pattern to the latter 2 worms. Peak burdens were encountered during April and October in the younger animals and a considerably higher peak during May in the older animals with a minor peak during September and November. In contrast to the younger animals, from which few 4th stage larvae were recovered, some of the older animals harboured a considerable number of these larvae (Fig. 3D). *H. bedfordi, Trichostronglylus thomasi* and *C. connochaeti* all exhibited a marked drop in numbers during the period June–August (Fig. 3B-D).

Only small numbers of *Gaigeria pachyscelis* were recovered and these were confined mainly to the animals 4–12 months of age. Fairly large numbers of 4th stage larvae were present in these animals during June and July

TABLE 1 The helminth parasites recovered from blue wildebeest in the Kruger National Park

Helminth species	Total numbers of helminths recovered			Percentage of animals infested
	4th stage larvae or immature worms	Adult worms	Total	
Agriostomum gorgonis	101	473	574	80,0
Cooperia connochaeti	11 415	37 578	48 993	85,5
Dictyocaulus viviparus	0	195	195	58,2
Gaigeria pachyscelis	150	163	313	49,1
Haemonchus bedfordi	1 978	19 401	21 379	92,7
Haemonchus contortus	0	50	50	1,8
Oesophagostomum sp.	89	408	497	69,1
Strongyloides sp.	0	6 452	6 452	25,5
Trichostrongylus axei	0	75	75	1,8
Trichostrongylus colubriformis	0	50	50	3,6
Trichostrongylus falculatus	0	175	175	1,8
Trichostrongylus thomasi	188	9 485	9 673	78,2
Trichuris sp.	0	1	1	1,8
Avitellina sp.	14	49	63	34,5
Moniezia benedeni	32	36	68	29,1
Moniezia expansa	1	1	2	1,8
Stilesia hepatica	—	—	—	7,3
Cysticercus regis	—	—	—	34,5
Schistosoma sp.	0	8	8	12,7

TABLE 2 The oestrid fly larvae recovered from blue wildebeest in the Kruger National Park

Oestrid fly species	Total numbers of larvae recovered				Percentage of animals infested
	1st stage	2nd stage	3rd stage	Total	
Gedoelstia spp.	12 635	—	—	12 635	96,4
Gedoelstia cristata	—	277	421	698	58,2
Gedoelstia hässleri	—	529	870	1 399	96,4
Kirkioestrus minutus	364	253	1 476	2 093	94,5
Oestrus spp.	274	—	—	274	65,5
Oestrus aureoargentatus	—	534	482	1 016	90,9
Oestrus variolosus	—	53	35	88	29,1

(Fig. 4A). *Agriostomum gorgonis*, also present in small numbers, reached peak burdens towards the end of the year in both age groups of wildebeest (Fig. 4B). A similar pattern was followed by *Oesophagostomum* sp. (Fig. 4C). The latter helminth appears to belong to an undescribed species.

M. benedeni first appeared in a 3-month-old animal and infestation was virtually confined to wildebeest under 12 months of age (Fig. 4D). *Moniezia expansa* was recovered only once, and then in a 4-month-old animal. *Avitellina* sp. was encountered for the first time in an 8-month-old animal and was subsequently present in animals of most age groups (Fig. 4D).

Oestrids

The species of oestrid fly larvae recovered, their abundance and prevalence are summarized in Table 2.

The larvae of 5 oestrid flies were recovered. No specific identifications of the 1st stage *Gedoelstia* spp. or 1st stage *Oestrus* spp. larvae were made, but, utilizing the numbers of 2nd and 3rd stage larvae recovered, *Kirkioestrus minutus* was the most abundant and *Gedoelstia hässleri* the most prevalent of the oestrid fly larvae. *Oestrus variolosus* was the least abundant and least prevalent species.

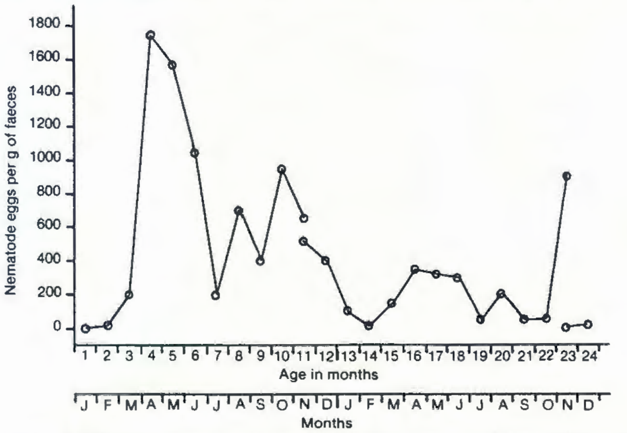

FIG. 2 The faecal worm egg counts of 1–24-month-old blue wildebeest in the Kruger National Park

The mean burdens of oestrid larvae of the wildebeest ranked by age are graphically illustrated in Fig. 5.

The youngest animals found harbouring 1st stage *Gedoelstia* spp. larvae were 2 months old. Burdens increased erratically thereafter and reached a peak in the 13-month-old animals. Animals older than this harboured considerably fewer 1st stage larvae (Fig. 5A,B). The majority of these 1st stage larvae were recovered on and in the dura of the cranial cavity. None were recovered from the eyes and only a few from the hearts and lungs. The 1st stage larvae recovered from the nasal cavities were considerably larger than those found elsewhere.

Wildebeest under 12 months of age harboured fewer 2nd and 3rd stage larvae of *Gedoelstia cristata* and *G. hässleri* than the older animals (Fig. 5A,B).

No clear pattern of prevalence was evident for *K. minutus* but burdens of 1st stage larvae reached a peak in the animals examined during November 1978 (Fig. 5C).

Larvae of *Oestrus aureoargentatus* reached peak numbers in the 7-month-old wildebeest during July. Burdens in the younger animals were generally considerably higher than those in the older ones (Fig. 5D). No clear pattern of seasonal prevalence could be established for *O. variolosus* as larvae of this fly were encountered erratically.

The lengths of the pupal periods of the mature oestrid larvae of the various species allowed to pupate in vermiculite are summarized in Table 3, as are the numbers of larvae collected and the numbers of flies that hatched.

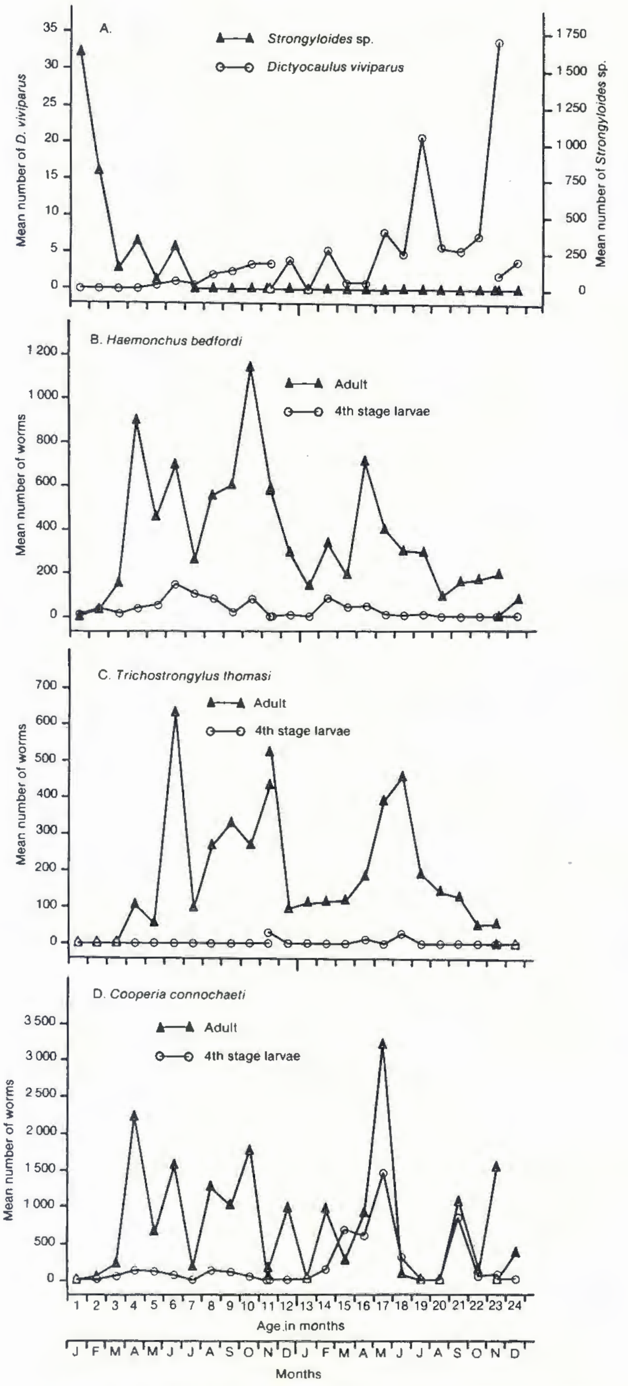

FIG. 3 The burdens of A *Strongyloides* sp. and *Dictyocaulus viviparus*
B *Haemonchus bedfordi*
C *Trichostrongylus thomasi* and
D *Cooperia connochaeti*
of 1–24-month-old blue wildebeest in the Kruger National Park

The pupal period of *G. cristata* ranged from 27–86 days, and that of *G. hässleri* from 20–57 days. The pupal period of *K. minutus* ranged between 31 and 53–58 days, that of *O. aureoargentatus* between 24 and 76 days and that of *O. variolosus* between 33 and 81–86 days. A high percentage of the *G. hässleri* and *O. aureoargentatus* larvae allowed to pupate gave rise to flies.

The species of lice and ticks and pentastomid nymphae recovered, and their abundance and prevalence are summarized in Table 4. The ectoparasite burdens of the 4 animals shot during November 1977 and 4 shot during May 1978 were not taken into account when compiling this table or the succeeding graphs as the skins of the former had been processed differently from those of the other animals and the skins of the latter had accidentally been discarded.

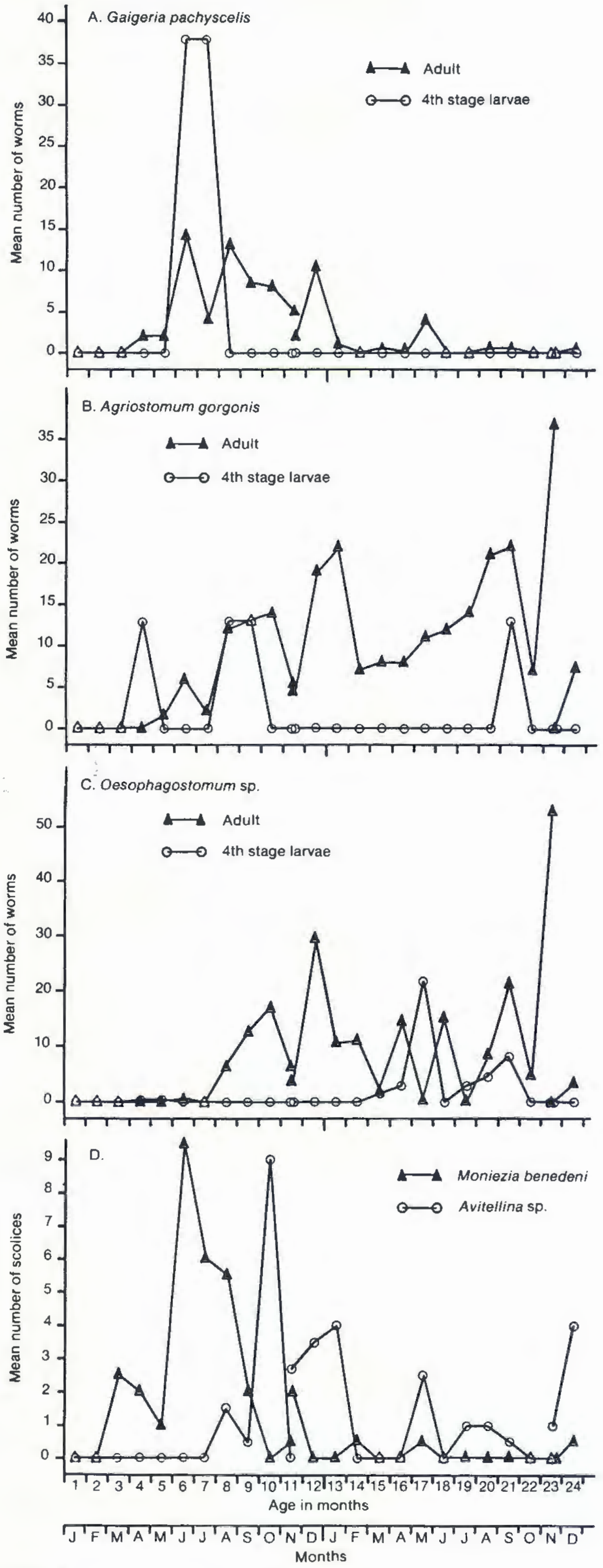

FIG. 4 The burdens of A *Gaigeria pachyscelis*
B *Agriostomum gorgonis*
C *Oesophagostomum* sp. and
D *Moniezia benedeni* and *Avitellina* sp.
of 1–24-month-old blue wildebeest in the Kruger National Park

Three lice species, 7 ixodid tick species, 1 mite species and the nymphae of a pentastomid species were recovered.

TABLE 3 The lengths of the pupal periods of oestrid fly larvae recovered from blue wildebeest in the Kruger National Park

Date mature 3rd stage larvae collected	Length of pupal periods in days				
	Gedoelstia cristata	*Gedoelstia hässleri*	*Kirkioestrus minutus*	*Oestrus aureoargentatus*	*Oestrus variolosus*
16 November 1977	27	21	—	24–25	—
13 December	27	21–22	—	27–28	33
16 January 1978	—	—	Failed to hatch	Failed to hatch	—
14 February	—	23	—	27	—
13 March	28–29	—	31–32	28–30	Failed to hatch
17 April	54–57	38–42	Failed to hatch	50–58	—
08 May	86	49–57	Failed to hatch	70–76	—
05 June	81–86*	—	Failed to hatch	70–73	81–86*
03 July	Failed to hatch	45–49	53–58*	58	—
07 August	Failed to hatch	35	44–46	43–44	—
11 September	—	28–32	37	—	—
16 October	33	25–29	33–38	32–35	Failed to hatch
15 November	—	20–21	Failed to hatch	—	—
Total number of mature 3rd stage larvae collected	20	43	36	37	10
Total number of flies hatched	9	35	12	28	4

* Exact day of hatching not determined

TABLE 4 The arthropod parasites recovered from blue wildebeest in the Kruger National Park

Arthropod species	Total numbers of arthropods recovered					Percentage of animals infested
Lice*		Nymphae	Adults		Total	
Damalinia theileri		1 053	562		1 615	89,4
Linognathus gorgonus		1 228	639		1 867	78,7
Linognathus spicatus		27	38		65	31,9
Ixodid ticks*	Larvae	Nymphae	Males	Females	Total	
Amblyomma hebraeum	3 439	188	11	4	3 642	87,2
Boophilus decoloratus	19 722	3 805	1 271	940 (88)	25 738	100,0
Hyalomma truncatum	0	0	5	1	6	5,9
Rhipicephalus appendiculatus/zambeziensis	2 455	—	—	—	2 455	55,3
Rhipicephalus appendiculatus	—	4 061	2	1	4 064	59,6
Rhipicephalus evertsi evertsi	2 180	72	39	28	2 319	83,0
Rhipicephalus simus	60	0	0	0	60	9,8
Rhipicephalus zambeziensis	0	21	0	0	21	25,5
Mites		Nymphae	Males	Females	Total	
Sarcoptes sp.		Numerous			Numerous	3,6
Pentastomids		Nymphae			Total	
Linguatula nuttalli		74			74	21,8

* Numbers based on 47 animals

() Number of female *B. decoloratus* between 4,0 and 7,0 mm in length

Lice

Linognathus gorgonus was the most abundant of the lice and *Damalinia theileri* the most prevalent.

The mean burdens of lice recovered from the wildebeest ranked by age are graphically illustrated in Fig. 6.

D. theileri reached peak numbers during April and September in both age groups of wildebeest, but the younger animals harboured considerably more lice than did the older ones. With few exceptions burdens of nymphae exceeded those of adult lice (Fig. 6A).

Peak numbers of *L. gorgonus* were recovered from February–April from 2–4-month-old wildebeest and during August and September from 8–9- and 20–21-month-old animals. Nymphal burdens virtually always exceeded adult burdens (Fig. 6B).

Only small numbers of *Linognathus spicatus* were recovered. These reached peak levels during August–October in both age groups of wildebeest and during February and March in 14–15-month-old animals. Adult burdens usually exceeded nymphal burdens.

Ticks

The larvae of *Amblyomma hebraeum* reached peaks during October and November in the 10-11-month-old wildebeest and during October in the 22-month-old animals (Fig. 7A). Very few adults and relatively small numbers of nymphae were recovered.

Boophilus decoloratus was the most abundant and the most prevalent of the tick species recovered. Few *B. decoloratus* reached the nymphal stage and only about half the nymphae reached adulthood (Table 4). Peak burdens were encountered during the period April–June in both groups of animals (unfortunately the hides of the animals culled in May were not examined) and during October in the younger animals and September and October in the older ones (Fig. 7B).

Rhipicephalus appendiculatus and *Rhipicephalus zambeziensis* larvae were both present but differential counts of these larvae were not made. The larvae of these ticks reached peak numbers from May–September and the nymphae of *R. appendiculatus* from June–October in both groups of wildebeest (Fig. 7C). A total of only 3 adult *R. appendiculatus* were recovered.

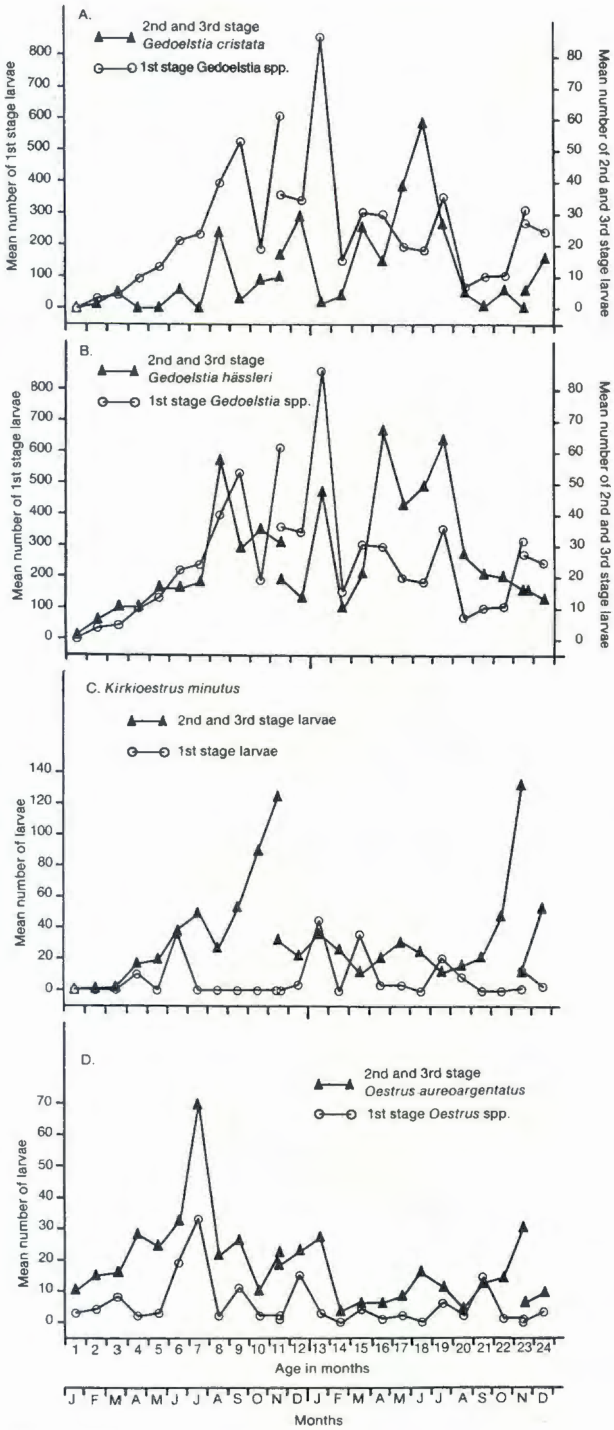

FIG. 5 The burdens of A 2nd and 3rd stage *Gedoelstia cristata* larvae and 1st stage *Gedoelstia* spp. larvae
B 2nd and 3rd stage *Gedoelstia hässleri* larvae and 1st stage *Gedoelstia* spp. larvae
C *Kirkioestrus minutus* larvae and
D 2nd and 3rd stage *Oestrus aureoargentatus* larvae and 1st stage *Oestrus* spp. larvae
of 1–24-month-old blue wildebeest in the Kruger National Park

The larvae of *Rhipicephalus evertsi evertsi* reached a major peak during the period April—June and a minor peak during October in both age groups of animals (Fig. 7D). Few nymphae and even tewer adults were recovered.

The mean monthly minimum and maximum temperatures and total monthly rainfall at Skukuza are graphically illustrated in Fig. 8.

The highest maximum temperatures were recorded during November and December 1977 and during November 1978. The lowest minimum temperatures were recorded during June and July 1978. Rainfall was concentrated in the spring and summer months from October to April. Little or no rain fell in the months between May and September.

Black wildebeest

The parasite burdens of the 7 black wildebeest examined in the Golden Gate Highlands Park are summarized in Table 5.

Three species of nematodes, 1 cestode, the larvae of an oestrid fly, 2 species of lice, 1 tick and 1 mite species were recovered. All the animals were infested with *H. bedfordi,* the 2 younger animals harbouring considerably more worms than the older ones. All the wildebeest were also infested with the larvae of *G. hässleri,* the majority of 1st instar larvae of this fly being recovered from the dura surrounding the cranial cavity.

The parasite burdens of the 3 black wildebeest shot in the Rietvlei Nature Reservè are summarized in Table 6.

Three nematode species, the larvae of 4 oestrid fly species and 3 ixodid tick species were recovered. In common with the black wildebeest in the Golden Gate Highlands Park these wildebeest were infested with *H. bedfordi* and *Oesophagostomum columbianum.* No *Gedoelstia* sp. larvae were recovered from their cranial cavities.

DISCUSSION

Of the numerous parasites recovered, only *H. bedfordi* and *G. hässleri* were recovered in large numbers from a substantial number of both blue and black wildebeest.

Blue wildebeest

Coccidia

The lower coccidial faecal oocyst counts in the older group of wildebeest are probably an indication of resistance to infection acquired by these animals. Part of this decrease may also be due to the larger volume of faeces excreted by the older animals and hence dilution of the oocysts.

Helminths

The nematode faecal egg counts were highest in the 1–6-month-old animals, and the counts in the 7–12-month-old animals were in turn higher than those in the 13–18-month-old animals. In the latter group of wildebeest, the egg counts were more sustained than in the 19–24-month-old animals. Although the decrease in faecal egg counts in the older animals is possibly due to increased faecal volume, it is more likely that it is due to increased resistance to infestation resulting in a decrease in faecal egg output by the female worms (Roberts, O'Sullivan & Riek, 1952; Michel, 1963). This supposition is borne out by the fact that, although the total accumulated burdens of *H. bedfordi, Trichostrongylus thomasi* and *C. connochaeti* (the 3 major nematode parasites) were reasonably similar during each 6-month period of the wildebeests' lives until they reached 18 months of age, the faecal worm egg counts decreased progressively during each of these 3 periods. Despite this decrease, the faecal worm egg counts can be related to the worm burdens of these 3 species in that low worm burdens and low egg counts were present during December or January and during July or August (Fig. 2 & 3).

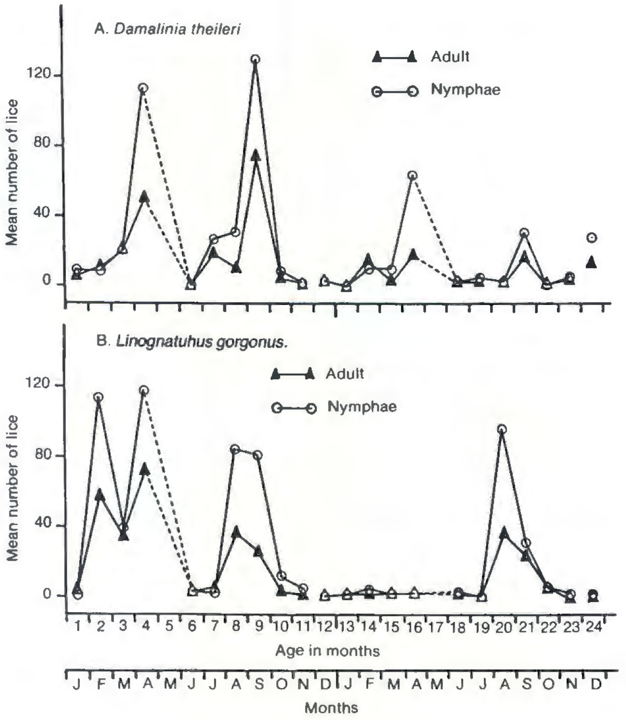

FIG. 6 The burdens of A *Damalinia theileri* and B *Linognathus gorgonus* of 1–24-month-old blue wildebeest in the Kruger National Park

D. viviparus is the common lungworm of cattle (Levine, 1968). However, it has also been recovered from moose (Gupta & Gibbs, 1971), elk (Presidente, Worley & Catlin, 1972), black-tailed deer (Presidente & Knapp, 1973) and from blue wildebeest in the Kruger National Park (Ortlepp, 1962). In South Africa it had been considered as a parasite found in cool, moist environments (Ortlepp, 1962) and hence the Kruger National Park with its hot, and relatively dry climate seems an unlikely habitat. The latter fact probably accounts for the small numbers of worms recovered.

After an initial infestation with *D. viviparus* cattle may rapidly acquire immunity to reinfestation (Soulsby, 1965). In the wildebeest, however, there was a tendency for burdens to increase with age. It is probable that this occurred because the numbers of worms present in the initial infestations were insufficient to stimulate immunity.

In the Transvaal adult *Haemonchus contortus* and adult *Haemonchus placei* are encountered mainly during summer (November or December–March or April) in sheep and cattle respectively (Horak, 1981). In the Kruger National Park, however, *H. bedfordi* appears to be an autumn and spring parasite (Fig. 3B). A seasonal pattern, probably induced by the very hot summers and the cooler weather encountered during mid-winter, with milder temperatures during autumn and spring, was established (Fig. 8). The cooler weather of autumn and winter was not so rigorous as to result in a seasonal arrest in larval development in the host as is encountered with *H. contortus* and *H. placei* in sheep and cattle on the Transvaal Highveld (Horak, 1980).

Although the 1–12-month-old and 13–24-month-old wildebeest were generally shot on the same day and in the same habitat and were thus exposed to the same degree of infestation, this was not reflected in their burdens of *H. bedfordi*. These burdens in the 8–11-month-old animals, shot during August–November, were relatively large, while those of the 20–23-month-old animals (August–November) were very low and, in addition, few if any larvae became established. A clear age resistance to infestation had developed in these animals.

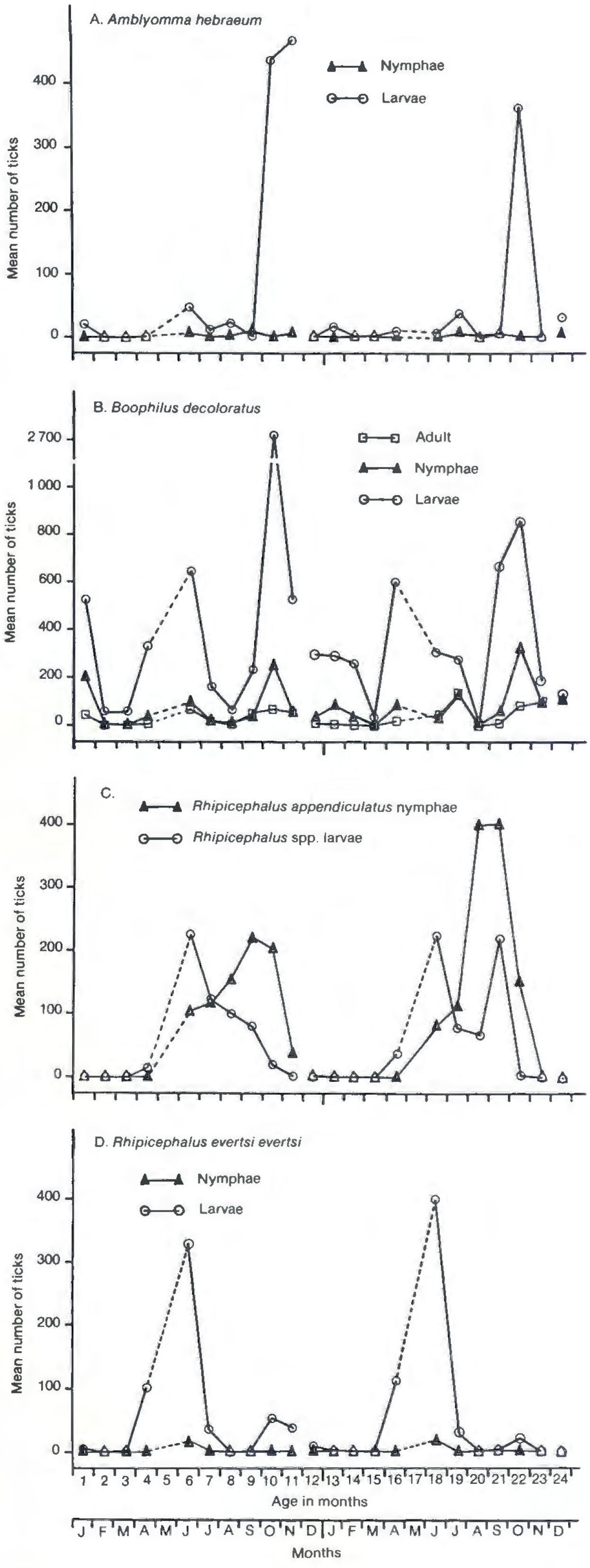

FIG. 7 The burdens of A *Amblyomma hebraeum*
B *Boophilus decoloratus*
C *Rhipicephalus appendiculatus* nymphae and *Rhipicephalus* spp. larvae and
D *Rhipicephalus evertsi evertsi*
of 1–24-month-old blue wildebeest in the Kruger National Park

TABLE 5 The endo- and ectoparasite burdens of black wildebeest in the Golden Gate Highlands Park

Age of animals	Number of parasites recovered													
	Helminths					Arthropods								
	Haemonchus bedfordi		*Oesophagostomum columbianum*	*Trichuris* sp.	*Thysaniezia* sp.	*Gedoelstia hässleri*			*Damalinia* sp.		*Linognathus* sp.	*Rhipicephalus* sp.	*capensis*	*Chorioptes* sp.
	4th	Adult	Adult	Adult	Scolices	1st	2nd	3rd	Nymph	Adult	Adult	Larvae	Adult	
March 1979														
15 months	253	925	1	0	0	501	7	44	6	5	1	0	0	—
Adult	28	153	0	0	0	124	5	47	0	0	0	0	1	—
Old	3	27	0	0	0	80	0	2	0	1	0	0	0	Positive
Old	30	226	1	0	0	218	7	29	2	5	0	1	0	—
December 1979														
24 months	52	1 480	4	1	1	32	5	16	2	4	0	0	0	—
Adult	0	52	0	0	0	260	7	37	0	0	0	0	0	—
Adult	0	77	4	0	0	222	8	32	0	1	0	0	0	—

1st, 2nd, 3rd, 4th = 1st, 2nd, 3rd, 4th stage larvae

TABLE 6 The endo- and ectoparasite burdens of black wildebeest in the Rietvlei Nature Reserve

Date slaughtered	Numbers of parasites recovered																		
	Helminths			Oestrid larvae								Ixodid ticks							
	Haemonchus bedfordi		*Oesophagostomum columbianum*	*Gedoelstia* sp.			*Kirkioestrus minutus*	*Oestrus macdonaldi*		*Oestrus variolosus*		*Boophilus decoloratus*		*Hyalomma truncatum*		*Rhipicephalus evertsi evertsi*			
					G. cristata														
	4th	Adult	Adult	1st	2nd	3rd	1st	2nd	3rd	2nd	3rd	♂	♀	♂	♀	L	N	♂	♀
6 Jul 1981	275	1 400	24	1	1	0	241	2	2	37	119	4	16	0	0	160	52	3	3
17 Jul 1981	150	250	22	0	0	0	30	0	0	14	20	0	0	1	0	176	72	2	4
*31 Aug 1981	717	667	118	3	4	10	8	0	0	18	44	0	0	0	2	460	12	3	2

1st, 2nd, 3rd, 4th = 1st, 2nd, 3rd, 4th stage larvae
* 1 Adult *Trichostrongylus axei*
L = larvae
N = nymphae

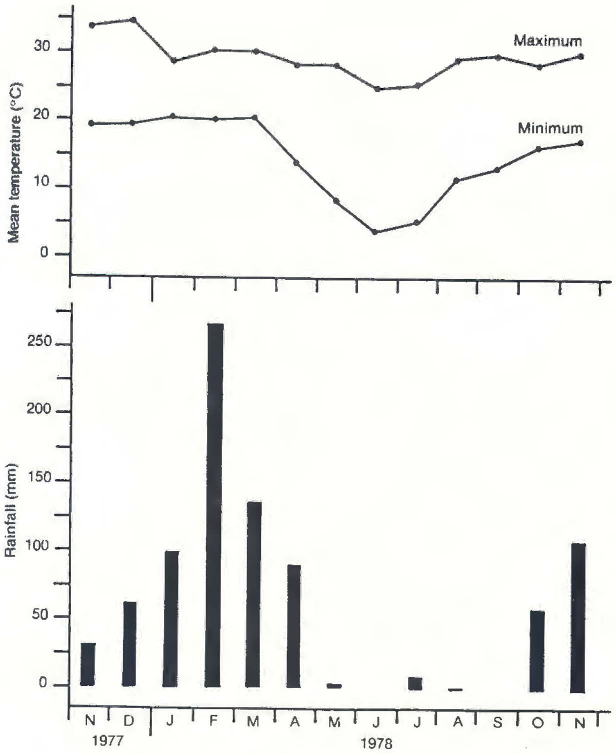

FIG. 8 The monthly mean minimum and maximum atmospheric temperatures and monthly rainfall at Skukuza from November 1977–November 1978

The burdens of *Trichostrongylus thomasi*, an abomasal parasite like *H. bedfordi*, closely followed the seasonal pattern exhibited by the latter worm. Peak burdens were, however, only attained 1 or 2 months after *H. bedfordi* had passed its respective peaks (Fig. 3B,C). It is interesting to speculate whether the rise in the numbers of *Trichostrongylus thomasi* caused a decline in the numbers of *H. bedfordi* or whether *Trichostrongylus thomasi* could only reach peak burdens once the numbers of *H. bedfordi* had started to decline. In either event this implied that the adult worms of these 2 species were not competing for space in the abomasum at the same time.

Reinecke (1974) has demonstrated that large burdens of *H. contortus* and *Trichostrongylus axei* compete for space in the abomasa of sheep to the detriment of the former worm. The staggered peaks of *H. bedfordi* and *Trichostrongylus thomasi* recorded in the present survey might be due to such competition. A marked resistance to reinfestation with *Trichostrongylus thomasi* was apparent once the animals reached 20 months of age.

C. connochaeti is a parasite of blue wildebeest recently described by Boomker, Horak & Alves (1979). Its burdens followed a pattern very similar to those of *H. bedfordi* (Fig. 3B,D), but immunity in the 20–24-month-old animals was not as marked. Immunity to reinfestation was, however, also present and was evident in the delay in development of 4th stage larvae to adulthood and their presence in fairly large numbers in some animals over 13 months of age. This phenomenon was absent in the younger animals.

The pattern of infestation with *Strongyloides* sp. seems to indicate a milk-borne infestation as is encountered with *Strongyloides papillosus* in sheep and goats (Moncol & Grice, 1974).

G. pachyscelis is a parasite of sheep (Ortlepp, 1937) and impala (Heinichen, 1973), and its presence in the wildebeest could be due to the large numbers of impala present in the Kruger National Park. A solid immunity to reinfestation develops in sheep (Horak, 1971). A similar phenomenon may account for the virtual disappearance of worms of this species once the wildebeest had reached 13 months of age (Fig. 4A). Horak (1971) also noted that in sheep a prior infestation with *Dictyocaulus filaria* interfered with the establishment of a subsequent infestation with *G. pachyscelis*. It is possible that the increasing burdens of *D. viviparus* in the older wildebeest interfered with the establishment of *G. pachyscelis* in these animals, thus accounting for the small burdens of the latter worm. It is also interesting to note that Horak (1971) stated that cross-immunity between *D. filaria* and *G. pachyscelis* was of little epizootiological significance in South Africa, as he then erroneously thought that worms of the former genus were confined to the cooler, moister regions of the country and those of the latter to the semi-arid western half of the country.

A. gorgonis appears not to be affected by previous infestation with its own kind or by that with *D. viviparus* and worms reached peak numbers towards the end of the year in both age groups of wildebeest (Fig. 4B). As the life cycle of this worm has to our knowledge not been determined it is possible that it passes neither through the skin nor lungs, both of which are barriers to reinfestation with *G. pachyscelis* in the immune sheep (Horak, 1971).

The *Oesophagostomum* sp. recovered also appears to reach peak numbers towards the end of the year and 4th stage larvae are encountered more frequently in older than in younger animals (Fig. 4C).

M. benedeni is a parasite of young wildebeest which appear to become solidly immune to infestation in their 2nd year of life. Infestation is acquired mainly during late summer and winter (Fig. 4D). *Avitellina* sp. affects slightly older animals and these acquire their infestation during springs and summer (Fig. 4D). This pattern of infestation means that these cestodes do not compete for space in the small intestine of the wildebeest.

Lions are the final host of *Taenia regis* and wildebeest can serve as hosts for the cysticerci of this worm. The large number of wildebeest infested with *Cysticercus regis* is an indication of the overlap that occurs between the habitat of wildebeest and lion in the Park.

The majority of *Schistosoma* sp. were recovered from the livers of the wildebeest. As no methods for the specific recovery of *Schistosoma* species were employed, the prevalence of infestation found in this survey cannot be taken as an accurate reflection of the true picture.

Oestrids

Although Basson (1962) has described the 1st stage larvae of *G. cristata* and *G. hässleri*, no attempt was made to differentiate the large numbers of 1st stage *Gedoelstia* spp. larvae recovered in the present survey. Wildebeest over approximately 13 months of age apparently develop a degree of resistance to infestation with 1st stage *Gedoelstia* spp. larvae as burdens decrease markedly after this age (Fig. 5A,B). At the same time larger numbers of 2nd and 3rd stage larvae became established in the older animals, possibly because of the greater space available in the sinus cavities of these animals.

The erratically increasing burdens of 1st stage *Gedoelstia* spp. larvae in the younger animals suggest that these larvae accumulate on the dura mater. Few of these larvae, or those encountered in the older animals, develop any further, judging by the relatively small numbers of 2nd and 3rd larvae recovered. Large numbers of 1st stage larvae are probably destroyed and resorbed before they can return to the sinus cavities, thus resulting in the disparity in numbers between the 1st and other stages.

Although no 1st stage *Gedoelstia* spp. larvae were encountered on the cornea of the eyes of any of the wildebeest, there seems little reason to doubt that this is the site on which they were deposited, as described by Basson (1966) and Horak & Butt (1977). In the present survey, the vast majority of larvae followed the ocular-cranial route to reach the nasal cavity in preference to the ocular-vascular-pulmonary route (Basson, 1966; Horak & Butt, 1977). In Zambia, however, Howard (1976) failed to recover 1st stage *Gedoelstia* sp. larvae from the brain surfaces of several blue wildebeest he examined.

The pupal periods of *G. cristata* were always longer than those of *G. hässleri*, with the differences becoming more pronounced as the mean monthly temperatures dropped. Possibly the mature *G. cristata* larvae which were collected during July and August 1978 failed to hatch (Table 3) simply because the temperatures were too low.

The mature 3rd stage larvae of *G. hässleri* pupated and flies hatched throughout the year. The pupal periods for the corresponding months of the year were always shorter than those recorded for this fly on the Transvaal Highveld by Horak & Butt (1977). In their survey larvae collected from May—July failed to develop into adults because of the lower temperatures. Not only were the pupal periods of *G. hässleri* shorter than those of *G. cristata* in the present survey but a considerably greater proportion of the mature larvae gave rise to flies. This indicates a shorter generation time and more successful survival rate for the former fly.

The specimens and data obtained in this survey were used by Horak, Boomker & De Vos (1980) for their descriptions of the larval stages of *K. minutus* and its life cycle and seasonal prevalence. This information will not therefore be discussed further here. Howard (1976) recovered no *K. minutus* from blue wildebeest in Zambia.

O. aureoargentatus is a parasite found in several antelope species belonging to the Alcelaphinae and Hippotraginae (Zumpt, 1965). Its life cycle is probably very similar to that of *Oestrus ovis* in sheep, in which 1st stage larvae are deposited in the nostrils, develop to mature 3rd stage larvae in the sinus cavities and then crawl out to pupate (Horak, 1977). It differs from that of *Oestrus macdonaldi* and *O. variolosus* in blesbok in that its 1st stage larvae do not undergo a pulmonary migration before they return to the naso-pharyngeal area (Horak & Butt, 1977).

The development of *O. aureoargentatus* to the 3rd larval stage appears to be rapid because 1 of the 1-month-old wildebeest calves examined already harboured 16 3rd stage larvae. Young wildebeest harboured more *O. aureoargentatus* larvae than older animals. A similar observation has been made with *O. ovis* infestation in sheep (Horak, 1977). The relatively large numbers of 3rd stage *O. aureoargentatus* larvae recovered compared with the numbers of 1st stage larvae present indicated that little mortality occurred during development. Mature 3rd stage larvae were able to pupate and give rise to flies throughout the year, so they could probably infest animals at any time. The pupal periods were always longer than those of *G. hässleri* collected during the same months. They were approximately the same as those of *G. cristata*, except during the colder months when they were slightly shorter (Table 3). As in the case of *G. hässleri* a very high percentage of mature larvae gave rise to flies.

Few *O. variolosus* were recovered and no seasonal or age pattern of infestation was apparent. Pupal periods were longer than those of *O. aureoargentatus* larvae collected during the same months.

Despite the many species and large numbers of oestrid larvae recovered from various sites in the heads of the wildebeest little reaction to infestation was evident. When many larvae were present on the dura mater it was sligthly thickened and opaque, while when many were present in the sinus cavities a slight serous or sero-purulent sinusitis was present.

Lice

Each of the 3 species recovered exhibited a very distinctive pattern of prevalence. A clear age resistance to the establishment of *D. theileri* is evident in the older wildebeest, but despite this, infestation reached peak numbers in autumn and spring in boths age groups of animals. In the case of *L. gorgonus* peak burdens were also present in autumn and spring in the young animals. The autumn burdens were, however, completely absent in the older animals, probably because of age resistance. Their reappearance in spring is possibly due to a breakdown of this resistance because of poorer nutrition during the winter months. *L. spicatus*, although present in only very small numbers, exhibited late summer and spring peaks; the older animals, however, harboured more lice of this species than the younger ones.

Ticks

Probably one of the most remarkable findings of this survey was that very few adult ticks of any species, excepting *B. decoloratus*, were found on the blue wildebeest. Even with the blue tick few larvae reached adulthood, judging by the relative numbers of each stage present. Wagland (1979) has also demonstrated a marked difference between larval and nymphal numbers on resistant cattle infested with *Boophilus microplus*. A large proportion of the females of *B. decoloratus* that we collected had, however, reached a length of over 4,0 mm. This is only slightly shorter than the 4,5 mm given by Wharton & Utech (1970) for *B. microplus* females that will complete their engorgement and detach within 24 h.

B. decoloratus exhibited 2 seasonal peaks on both age groups of wildebeest. The loss of the hides of the animals culled during May prevents an estimation of the magnitude of the autumn peak but the spring peak was considerably higher on the young animals than on the older ones. We do not know whether this was fortuitous or due to acquired resistance in the older animals.

Baker & Dukasse (1967) recorded the greatest activity of all stages of *B. decoloratus* on cattle in Natal during the period November–June, while MacLeod, Colbo, Madbouly & Mwanaumo (1977) noted a major peak in adult numbers on cattle in the Central Province of Zambia during April–June and a minor peak during October and November. Robertson (1981) recorded peak numbers of *B. decoloratus* on cattle in the eastern Cape Province from February–June.

Horak (1982) commented that very few adult ticks were recovered from impala running with cattle, but he found that the impala were efficient hosts of the immature stages. He recovered a total of only 221 adult *R. appendiculatus* and 99 adult *R. evertsi evertsi* from 36 impala, as opposed to 3 166 and 689 respectively from 24 cattle, examined in a nature reserve in the northern Transvaal. In the present survey only 3 adults of the former and 67 adults of the latter tick were recovered from the 47 wildebeest examined. Apparently, therefore, the blue wildebeest is an even poorer host of the adults of these ticks than impala.

Further examination of the tick burdens shows that, except for *R. appendiculatus,* the wildebeest is also a poor host of tick nymphae. The conclusions of Yeoman & Walker (1967) that all stages of *R. appendiculatus* thrive on cattle, and that medium-small wild animals only seem to carry nymphae when there are cattle infested with this tick in the area, allow for 2 suppositions in the present survey. Firstly, that some host other than wildebeest carried large burdens of adult *R. appendiculatus* and, secondly, that blue wildebeest must be classified amongst the small-medium sized hosts of the immature stages of this tick. One of us (I.G.H.) has found that many host species (blesbok, impala, blue wildebeest, zebra, kudu, buffalo and cattle) he has examined, using the methods of tick recovery described earlier, are efficient hosts of the immature stages of *R. appendiculatus*. Several of the large species of animals such as kudu, buffalo and giraffe that abound in the Kruger National Park probably serve as hosts of the adult ticks.

No attempt was made to differentiate the larvae of *R. appendiculatus* from those of *R. zambeziensis*. The May–September peak of these 2 species of larvae is later than the March/April–July peak for the *R. appendiculatus* larvae recorded on impala and cattle in the northern Transvaal by Horak (1982). The nymphal peak, from June–October, is the same in both areas. Both peaks are, however, later than the February–June and April–September peaks recorded for larvae and nymphae respectively on cattle in Natal by Baker & Ducasse (1967). In the eastern Cape Province, Knight & Rechav (1978) found that larvae reached peak numbers on greater kudu from May–June and nymphae from May–June and August–October.

During the normal life cycle of the 2 host tick *R. evertsi evertsi* the larvae and nymphae share the same host, but on the blue wildebeest very few larvae reached the nymphal stage, thus apparently abruptly ending the cycle.

Although the upper legs, bodies and necks of the wildebeest shot during May were not examined, their ears and heads were. As the majority of immature *R. evertsi evertsi* are recovered from the ears and heads of animals the burdens of this tick recovered from the animals shot during May can be taken as close to the actual total. Fewer than 5 ticks of this species were recovered from the ears and heads of each of the animals examined in May.

Horak (1982) noted that impala in the northern Transvaal were good hosts of both the larvae and nymphae of *R. evertsi evertsi*. He recorded peak larval burdens of *R. evertsi evertsi* on these animals from May–July (a slight drop in numbers occuring during June). The larval peaks recorded in the present survey showed a similar pattern but were very much more abrupt.

Horak (1982) noted that on cattle also, few *R. evertsi evertsi* larvae seemed to reach the nymphal stage, a fact he ascribed to the fortnightly use of an acaricide. In the light of the findings of the wildebeest further investigations concerning this tick on cattle seem warranted.

The larvae of *A. hebraeum* reached peak numbers on the younger wildebeest during October and November and during October only on the older animals. This pattern of infestation differs from that described by Horak (1982) for this tick on cattle and impala in the northern Transvaal. In that survey he found that November–March was the most favourable period for the larval stages. This differs considerably from the period February–May recorded by Baker & Ducasse (1967) on cattle in Natal and by Horak (unpublished data, 1981) on warthog in the Kruger National Park. It may well depend on the migratory habits of the wildebeest: the animals shot during October were culled in the southern region of the survey area just before they migrated northwards and those shot during November were in the northern region of the area just after they had completed their migration. It is possible that during this migration they were exposed to greater numbers of *A. hebraeum* larvae and that this was subsequently reflected in their tick burdens. Surveys that are being conducted on warthog, zebra, impala and kudu in the Kruger National Park may throw further light on the seasonal prevalence of this tick in this area.

Pentastomid

The recovery of the nymphae of *Linguatula nuttalli* from a large number of the wildebeest is, as in the case of the cysticerci of *Taenia regis,* an indication of the large number of lions, the final hosts of this pentastomid, in the Park.

Miscellaneous

The possible effect that the wildebeest migration may have had on the burdens of larval *A. hebraeum* has already been discussed but, as this migration may have affected other parasites too, it is worth further discussion.

The southern region of the study area, described as Lowveld by Acocks (1975), is a characteristic open *Acacia nigrescens-Sclerocarya* Savanna with a tall form of *Themeda triandra* as the dominant grass. The northern region described as Arid Lowveld, is typically an *Acacia nigrescens-Sclerocarya* Savanna, but with *Digitaria* sp. taking over the role of dominant grass from *T. triandra* (Acocks, 1975).

The majority of the wildebeest within the study area were present in the northern region from November–July and all our animals were shot within this region during these months. They migrated to the southern region of the area during July and all animals were shot here from August–October. During October they migrated back to the northern region.

A number of helminth and arthropod parasites had seasonal prevalences which could have been due either to climatic influences alone or to climatic and migratory interactions. These parasites had peaks in autumn, but dropped to a low level in July, just prior to the southern migration, followed by a peak in the spring with a decrease just before or at the time of the northern migration. Helminths which exhibited this pattern were, *H. bedfordi, Trichostrongylus thomasi* and *C. connochaeti*.

It is interesting to speculate whether the spring rise in burdens would still have occurred had the animals remained in the northern region and not migrated south. The spring rise implies that infective larvae of these 3 nematodes were either already present on the grazing in the south or that the wildebeest brought the infestation with them and the grazing rapidly became contaminated. Impala also harbour these 3 nematodes, although they are rarely infested with *H. bedfordi* and *C. connochaeti*. These animals abound in the park and could be responsible for contaminating the pastures in the southern region. However, the residual burdens in the wildebeest probably also contributed to this contamination.

This pattern of seasonal prevalence also appeared to apply to the *O. aureoargentatus* larvae. However, these fly larvae showed a marked drop in the young animals after the southern migration and did not rise again to the same high levels as those present before the migration.

Of the ticks, other than *A. hebraeum*, which has already been discussed, *B. decoloratus* exhibited a clear autumn peak on the wildebeest in the northern regions and a spring peak on these animals once they had reached the south.

The burdens of *R. appendiculatus/zambeziensis* larvae and *R. appendiculatus* nymphae are of particular interest in that the majority of the larvae were acquired during autumn in the northern region and the majority of the nymphae in spring in the southern region. This implies that the majority of adult ticks which gave rise to the larval and nymphal burdens respectively belonged to 2 geographically separate populations, 1 sustained on various animals in the northern region of the survey area and the other on animals in the southern region. These animals probably also sustained the larvae and nymphae of those ticks in these regions with the wildebeest acting as an additional host for larvae in the autumn in the north, and for nymphae in the spring in the south.

Peak numbers of larvae of *R. evertsi evertsi* were recovered from the wildebeest during April and June, just prior to their southern migration, with a minor peak during October, just before the migration northwards. One of the major sources of this tick was undoubtedly zebras as they are often sympatric with blue wildebeest and frequently carry large numbers of adult *R. evertsi evertsi* (Horak, unpublished data 1981). As adult *R. evertsi evertsi* are present throughout the year (Londt, Horak & De Villiers, 1979; Horak, 1982) it is not surprising that larvae were available in both regions.

All species of lice exhibited a peak on the wildebeest while they were in the north and another while they were in the south. As lice are permanent parasites it is unlikely that their seasonal prevalence is affected by the migrations of the wildebeest; they are probably controlled by climatological changes and the resistant status of the host.

The parasite burdens of 1 of the 6-month-old wildebeest are worth noting. This animal had broken a leg approximately 4 weeks before it was shot for survey purposes during June 1978. It harboured 575 adult *Strongyloides* sp. while its equal aged partner had none of these worms. It also harboured 175 adult *Trichostrongylus falculatus*, a nematode not found in any of the other wildebeest. It was infested with 2 071 *B. decoloratus*, of which more than 24 % had reached adulthood, compared with 390–805 ticks of this species, of which 4–12 % had reached adulthood, on the other 3 animals slaughtered at the same time. These differences in parasite burdens can probably be ascribed to a breakdown in the resistance of this animal brought about by the stress of a broken leg, and consequently the ectoparasite burdens of this animal have been excluded from the figures. In Australia stress has been shown to affect the resistance of cattle to the tick *B. microplus* (Utech, Seifert & Wharton, 1978). The difficulty this animal must have experienced with grooming may also account for the higher tick burdens.

Although numerous species of parasites were recovered from the blue wildebeest, the magnitudes of the burdens were such that they produced no readily detectable pathological changes; thus it did not appear as if parasites were the cause of the decline in the wildebeest numbers. A possible exception was *D. viviparus*, which occasionally caused fairly extensive pulmonary lesions. These lesions did not appear to be severe enough to cause death but may have debilitated the animals sufficiently to make them prone to capture by predators.

Black wildebeest

A small number of species and relatively small total numbers of helminths and ticks were recovered from the black wildebeest at both survey localities. This is probably a reflection both of the fairly cold climates prevalent in the regions in which the Golden Gate Highlands Park and Rietvlei Reserves are situated, and the fact that black wildebeest appear to be fairly resistant to parasitic infestation. *H. bedfordi*, however, appeared to be equally well-adapted to both blue and black wildebeest and to subtropical and temperate climates.

At Golden Gate a large proportion of the 1st stage larvae of *G. hässleri* were recovered from the subdural space and dura mater of the black wildebeest. This indicated that in this host, as in the blue wildebeest, the migratory pattern of the larvae of this fly is via the ocular-cranial-nasal route.

At Rietvlei considerably more *O. variolosus* larvae were recovered than either *G. cristata* or *O. macdonaldi* larvae. In 3 blesbok examined in the same reserve 1 or 2 months earlier the converse was true (Horak, Brown, Boomker, De Vos & Van Zyl, 1982). This difference could have been due to host preference or to seasonal variations in larval prevalence. *O. macdonaldi* has not previously been recovered from black wildebeest, so the low numbers present were possibly due to host preference. *K. minutus* had also not previously been recovered from black wildebeest.

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