Parasites of domestic and wild animals in South Africa. XLI. Arthropod parasites of impalas, *Aepyceros melampus*, in the Kruger National Park

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ABSTRACT

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Ectoparasites were collected from impalas, *Aepyceros melampus*, at four localities within the Kruger National Park, namely Skukuza, in the Biyamiti region, Crocodile Bridge and Pafuri. Animals were also examined at Skukuza during a severe drought and at Skukuza and Pafuri towards the end of a second drought. Parasite burdens were analysed in relation to locality, sex, age class, month and drought.

The impalas were infested with 13 ixodid ticks species, including two that were identified only to genus level. Except for four animals at Pafuri, all were infested with *Amblyomma hebraeum*. The highest intensity of infestation with larvae of this tick occurred from April to June and during November and December at Skukuza and in the Biyamiti region. Infestation with nymphs was highest during late winter. All animals were infested with *Boophilus decoloratus*, and the intensity of infestation was highest during spring. The intensity of infestation with *Rhipicephalus appendiculatus* was highest at Crocodile Bridge and at Pafuri, and that of *Rhipicephalus zambeziensis* at Skukuza. With both the latter species the intensity of infestation of larvae was highest from April to August, of nymphs from July to September or October and of adults during February and March. *Rhipicephalus kochi* was present only at Pafuri.

The impalas also harboured five louse species and two species of hippoboscid flies. The intensity of infestation with lice tended to be greater during late winter and spring than during other seasons and greater on lambs than on yearlings on which it was greater than on adult animals.

Keywords: *Aepyceros melampus*, drought, hippoboscid flies, impalas, intensity of infestation, ixodid ticks, Kruger National Park, lice, prevalence, seasonality

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INTRODUCTION

Impalas, *Aepyceros melampus*, are widely distributed in the eastern woodland regions of Africa, from northern Kenya south to northern KwaZulu-Natal, South Africa, with their southern distribution extending north-westward to south-eastern Angola and northern Namibia. They prefer light, open woodland communities and generally avoid open grassland unless it abuts on woodland (Skinner & Smithers 1990). Impalas are classified as intermediate mixed feeders as they both graze and browse (Skinner &

Smithers 1990), and within their range they are often the most numerous medium-sized antelopes. In South Africa they are present in national, provincial and privately owned nature reserves as well as on many mixed cattle and wildlife ranches.

With the possible exception of African buffaloes, *Syncerus caffer*, more surveys have been conducted on the arthropods infesting impalas than on those of any other wild African mammal. The ixodid tick species infesting impalas in sub-Saharan Africa have been listed by Theiler (1962); those in Kenya by Walker (1974); in Tanzania by Yeoman & Walker (1967); in Zambia by MacLeod (1970), Colbo (1973) and MacLeod & Mwanaumo (1978); in Botswana by Paine (1982); in Mozambique by Santos Dias (1993); in Swaziland by Gallivan & Surgeoner (1995); and in South Africa by Meeser (1952) and Baker & Keep (1970). Total, or calculated total tick burdens have been determined on these animals in Zambia (Zieger, Horak, Cauldwell, Uys & Bothma 1998), Zimbabwe (Colborne 1989; Mooring & McKenzie 1995; Mooring & Mazhowu 1995), Swaziland (Gallivan, Culverwell, Girdwood & Surgeoner 1995) and in South Africa in Limpopo Province (Horak 1982; Matthee, Meltzer & Horak 1997), Mpumalanga Province (Horak, Boomker, Kingsley & De Vos 1983c; Horak, Fourie & Van Zyl 1995c), North West Province (Van Dyk & McKenzie 1992) and KwaZulu-Natal (Horak, Keep, Flamand & Boomker 1988a). The louse species that infest impalas are listed by Ledger (1980), and their total louse burdens have been determined by Horak (1982), Horak *et al.* (1983c), Van Dyk & McKenzie (1992) and Matthee, Horak & Meltzer (1998). The flies recorded on these animals are listed by Haeselbarth, Segerman & Zumpt (1966).

The tick species infesting impalas are similar to those found on domestic cattle farmed in the same regions (Yeoman & Walker 1967; Walker 1974; Horak 1982; Colborne 1989), and those on sympatric antelope species (Gallivan & Surgeoner 1995; Horak 1998). Impalas appear to harbour larger tick infestations than other medium-sized antelope species (Gallivan & Horak 1997; Horak 1998), and may thus serve as an important reservoir of tick infestation on mixed cattle and wildlife farms (Horak 1982; Colborne 1989), and on game ranches or wildlife reserves, on which they are frequently the most numerous antelope species (Gallivan & Surgeoner 1995; Zieger *et al.* 1998). As lice are obligate permanent parasites, and those infesting impalas are host-specific, there is little possibility of cross-infestation with these parasites occurring with sympatric wild or domestic animals.

In this paper we compare the tick, louse and hippoboscid fly burdens of impalas examined in four landscape zones within the Kruger National Park (KNP). We also examine the seasonal intensity of infestation, and the relationships between infestation with the most abundant species of ectoparasites and host age and sex class.

MATERIALS AND METHODS

Survey animals

A total of 229 impalas were examined in several surveys in the Kruger National Park. Each animal was killed during the morning by a single shot in the neck from a small or large calibre rifle. The locations, seasons and age and sex classes of the animals are summarised in Table 1. Because parturition in these animals in southern Africa is generally confined to the months November to January (Skinner & Smithers 1990), it is possible to visually age impalas fairly accurately until the age of 2 years, particularly the males because of the age-associated changes in the shape of their horns. It is more difficult with the females that are hornless.

Parasite recovery

The impalas were processed for the recovery of arthropod parasites as described by Horak, Boomker, Spickett & De Vos (1992) for greater kudus, *Tragelaphus strepsiceros*. Ticks, lice and hippoboscid flies were collected from the processed material under stereoscopic microscopes, and identified and counted under the same microscopes. We estimate that the idiosoma of female *Boophilus decoloratus* would reach a minimum length of 4.0 mm 24 h before detachment, and the length of the idiosoma of engorging female ticks of this species was measured.

Survey localities

Skukuza (24°58'S, 31°36'E; Alt. 262 m)

Skukuza is a tourist rest camp, and is also the headquarters of the South African National Parks Kruger Park Management and Research divisions, situated in the south-western region of the KNP in a landscape zone described as Thickets of the Sabie and Crocodile Rivers (Gertenbach 1983) of which the vegetation is classified as Lowveld (Acocks 1988). The impalas examined in this region were shot within a 25 km radius of Skukuza. Three to seven animals were shot each month from January 1980 to January 1981, and always included a lamb (< 12 months of age), a yearling male (12– 23 months) and an adult (> 24 months). From February to May 1981 two to four animals were shot each month, always including an adult male and an adult female.

During the drought that occurred in 1982/83 a large number of impalas died from starvation in October and November 1982. Ten animals, considered terminally affected by the drought, were shot for survey purposes during these months. At the same time 14 apparently healthy animals were shot for comparison at the same locality. A severe drought occurred during 1991/92, and in March 1992 six 15-month-old impala males were shot and examined for parasites. Three yearling males were shot at the same locality and examined every month thereafter until April 1993.

Biyamiti region (25°06'–25°28'S, 31°25'–31°39'E; Alt. 200–350 m)

This survey site is located in the central southern region of the KNP in a landscape zone described as Mixed Bushwillow Woodlands (Gertenbach 1983) of which the vegetation is classified as Lowveld (Acocks 1988). It extended from north of the Biyamiti River to north of the Malelane entrance gate to the KNP. Each month from January 1980 to May 1981 two to six impalas, generally of the same ages and sexes as those shot at Skukuza, were shot in this locality and examined.

Crocodile Bridge (25°22'S, 31°54'E; Alt. 217 m)

Crocodile Bridge is a tourist rest camp close to the south-eastern border of the KNP. The vegetation is classified as Lowveld by Acocks (1988) and the landscape zone described as Marula/Knobthorn (*Sclerocarya caffra/Acacia nigrescens*) Savanna (Gertenbach 1983). Each month from January 1980 to January 1981 a single adult male impala was shot in the Crocodile Bridge region and examined for parasites.

Pafuri (23°27'S, 31°19'E; Alt. 305 m)

Pafuri is located in the far north-east of the KNP. The vegetation here is classified as Mixed Bushveld (Acocks 1988) and the landscape described as Limpopo/Levubu Floodplains by Gertenbach (1983). During July 1980, a lamb, a yearling, an adult male, and an adult female impala were shot and examined. From March 1992 to April 1993, three yearling males were shot and examined at 2–3 month intervals.

Climate

Monthly mean minimum and maximum atmospheric temperatures and total monthly rainfall were recorded at Skukuza, and are presented graphically in Fig. 1 for the periods 1979–1983 and 1990–1993.

Statistical analysis

Factors of interest in the analysis of the data were the effects of the location, season, age class, sex of the adult impalas, differences between years, and drought. However, because the collections were independent and factors were not balanced across studies it was not possible to analyse the data in a single multivariate analysis. Therefore, the data were subdivided and analysed in the following groups:

- Skukuza versus the Biyamiti region in 1980/81
- Skukuza, the Biyamiti region and Crocodile Bridge in 1980/81 (adult males only)
- Skukuza 1980/81 versus 1992/93
- Skukuza versus Pafuri in 1992/93
- Skukuza, Biyamiti and Pafuri in July 1980
- The 1982 drought

The factors analysed in each grouping are presented in Table 1. Differences in location and season were assessed by comparisons of the results of the individual analyses.

Most analyses compared both the prevalence and the intensity of infestation. Differences in prevalence were analysed using contingency tables with a x^2. For differences in the intensity of infestation, the parasite count data were logarithmically transformed to reduce the inequality of variance created by overdispersion (Petney, Van Ark & Spickett 1990). The data were then analysed using analysis of variance. In all of the analyses, factors were restricted to ensure equal balance among the groups. When factors were significant, a t-test was used to test between two groups and a Student-Newman-Keuls multiple range test was used to test among multiple groups. Because the 1980/81 and 1992/93 collections extended over 2 consecutive years and there was a potential for year-to-year variation, month was converted to a continuous variable starting in January of the first year (1980 or 1992). Animals less than 3 years old were aged to month; i.e., they were classed as lambs (0–11 months), yearlings (12–23 months) or adults (older than 24 months) in the analyses. In 1992/93, three to six yearling males per month were collected at Skukuza, and three

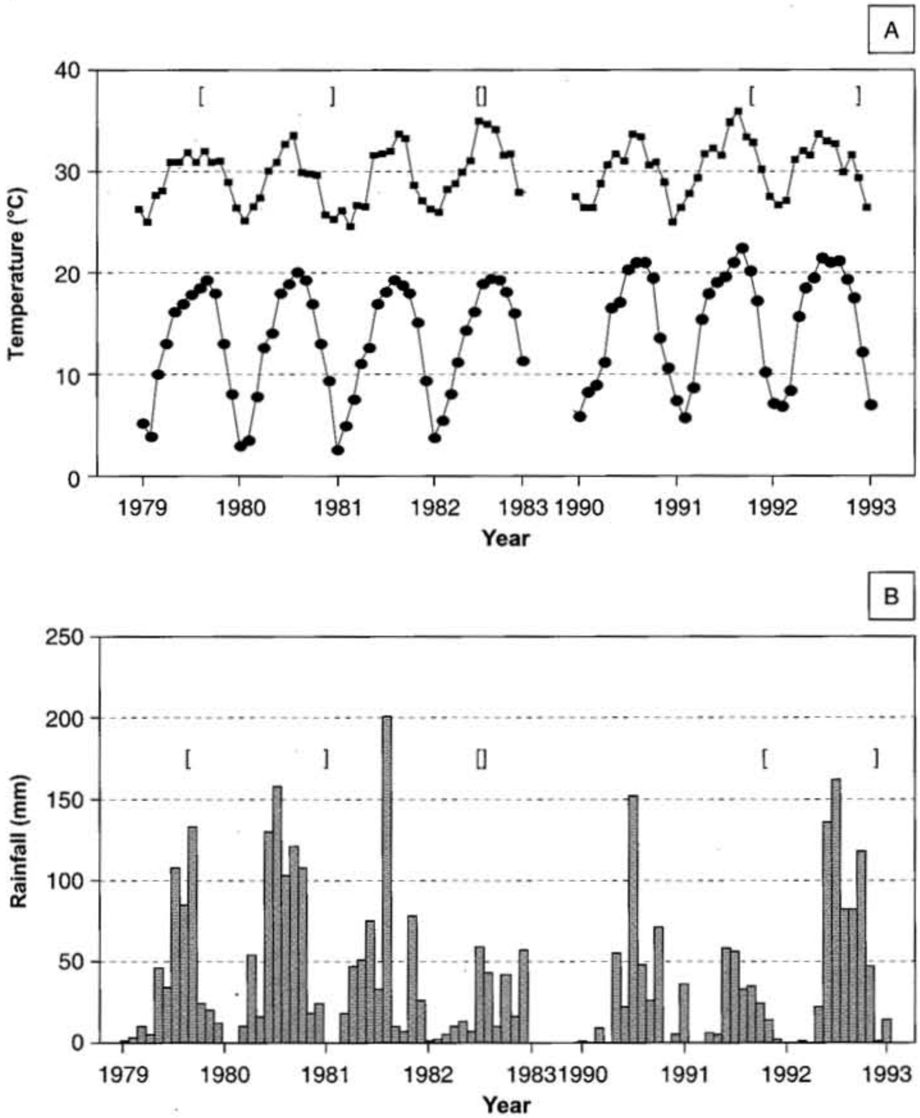

FIG. 1 [A] Average monthly minimum and maximum temperatures (°C) and [B] total monthly rainfall (mm) at Skukuza (1979–1983; and 1990–1993). Periods within brackets represent the survey periods

were collected at 2–3 month intervals at Pafuri. However, only one yearling was collected per month at Skukuza in 1980/81. To compare the parasite burdens at Skukuza in 1980/81 and 1992/93, the yearlings in 1992/93 were compared to the yearlings and adults in 1980/81 for the ticks, and to the lambs and yearlings for the lice. The groupings for 1980/81 were based on the results of the analysis for age effects. Because the 1982 drought potentially affected the parasite burdens of both the "terminal" and apparently healthy impalas, their parasite burdens were also compared to those from impalas collected during the same time period at Skukuza in 1980.

RESULTS AND DISCUSSION

IXODID TICKS

Total tick burdens

The impalas were infested with 13 species of ixodid ticks, of which 11 were identified to species level and two to genus level. Six species, *Amblyomma hebraeum, Amblyomma marmoreum, B. decoloratus, Rhipicephalus appendiculatus, Rhipicephalus evertsi evertsi* and *Rhipicephalus zambeziensis* were commonly collected at all locations, while *Rhipicephalus kochi* was only common at Pafuri (Table 2). The other species, *Amblyomma tholloni,*

TABLE 1 Groups, factors and ANOVA procedures used in the statistical analysis of the arthropod parasite burdens of impalas in the Kruger National Park

Group	Factors assessed	Statistical procedure	Comments
Skukuza vs Biyamiti	Location, month, age, sex	Three-factor ANOVAs: location, month and age; and location, month and sex	Location, month, age: month restricted to Jan 1980 to Jan 1981 Location, month, sex: adults only, month restricted to Mar 1980 to Apr 1981 (no adult females in Jan and Feb 1980)
Skukuza, Biyamiti and Crocodile Bridge	Location, month	Two-factor ANOVA	Adult males only, month restricted to Jan 1980 to Jan 1981
Skukuza 1980/81 vs 1992/93	Year, month	Two-factor ANOVA	Yearlings only in 1992/93 compared to yearlings and adults in 1980/81 for ticks; and to lambs and yearlings in 1980/81 for lice, months restricted to March 1980/92 to February 1981/93 (lice) or April 1981/93 (ticks)
Skukuza vs Pafuri 1992/93	Location, month	Two-factor ANOVA	Yearlings only, months matched to collections at Pafuri
Skukuza, Biyamiti and Pafuri	Location	One-factor ANOVA	July 1980 only, lamb, yearling and adults at each location
Skukuza 1982 drought	Group	One-factor ANOVA	"Terminal" vs "apparently healthy" impalas in 1982 compared to impalas collected in 1980 in same time period

TABLE 2 Proportional intensity of infestation of the major tick and louse species on impalas examined over a period of 12 months or more at four localities in the Kruger National Park

Arthropod species	Proportional intensity of infestation (%)				
	Skukuza (1980/81) (n = 63)	Skukuza (1992/93) (n = 45)	Biyamiti (1980/81) (n = 60)	Crocodile Bridge (1980/81) (n = 12)	Pafuri (1992/93) (n = 21)
Ticks					
Amblyomma hebraeum	24.07	25.05	10.56	21.49	6.31
Amblyomma marmoreum	0.60	1.38	0.05	0.14	0.07
Boophilus decoloratus	56.85	45.80	70.13	47.74	46.75
Rhipicephalus appendiculatus	2.13	0.64	5.37	24.03	15.82
Rhipicephalus evertsi evertsi	3.25	2.17	10.49	3.84	5.09
Rhipicephalus kochi	0.00	0.00	0.00	0.00	20.57
Rhipicephalus zambeziensis	13.08	24.95	3.39	2.75	5.34
Lice					
Damalinia aepycerus	18.57	22.75	21.02	10.05	18.93
Damalinia elongata	61.94	54.83	6.96	46.89	0.04
Linognathus aepycerus	11.35	18.14	34.53	42.82	65.20
Linognathus nevilli	6.58	3.17	33.68	0.24	14.33

n = Number of impalas examined

Haemaphysalis aciculifer, *Hyalomma truncatum*, *Ixodes* sp., *Rhipicephalus simus* and the *Rhipicephalus pravus* group were incidental or sporadic infestations (Tables 3–10).

The tick species infesting the impalas were similar to those collected from sympatric antelope species that had previously been examined in the KNP (Horak, Potgieter, Walker, De Vos & Boomker 1983a; Horak, De Vos & Brown 1983b; Horak *et al.* 1992; Horak 1998). Impalas appear to harbour disproportionately large tick burdens for their size (Gallivan & Horak 1997; Horak 1998), and the mean tick burden of the animals examined in the Biyamiti region was similar to the mean burden of greater kudus examined there 2 years later (Horak *et al.* 1992). However, a greater proportion of the ticks on the kudus consisted of adults, which supports the suggestion that larger ungulates are more important hosts for adult ticks (MacLeod 1970; Horak 1982). The tick burdens of the impalas would conceivably have been considerably larger if self-grooming, and probably also allogrooming, which are effective in removing ticks (A.A. McKenzie, unpublished data, cited by Hart & Hart 1992), are taken into account. Impalas are also one of the few smaller antelope species attended by red-billed oxpeckers, *Buphagus erythrorhynchus* (Stutterheim 1981), and these birds are capable of consuming large numbers of ticks (Bezuidenhout & Stutterheim 1980). In addition the method we used to collect ticks from the impalas was not the most efficient (Van Dyk & McKenzie 1992), but it did provide ticks, lice and flies that could all be identified.

The total tick burdens did not differ significantly among the locations, but there were differences in the prevalence and/or intensity of infestation of some species. These will be discussed in more detail below.

The total tick burden was significantly higher at Skukuza in 1980/81 than in 1992/93 ($P < 0.001$) (Table 11), and was higher at Pafuri in July 1980 than in August 1992 ($P < 0.1$). In contrast to 1992/93, the total tick burden of the impalas examined in 1980 at Skukuza was slightly higher than the burdens of the apparently healthy animals in the 1982 drought. The "terminal" impalas in 1982 had higher total tick burdens than the apparently healthy animals killed

TABLE 3 Arthropod parasites collected during 1980/81 from 63 impalas at Skukuza, Kruger National Park

Arthropod species	Number of arthropods collected				Total	Proportional abundance %	No. of impalas infested
Ixodid ticks	Larvae	Nymphs	Males	Females			
Amblyomma hebraeum	57 227	7 985	52	8	65 272	24.07	63
Amblyomma marmoreum	1 605	21	0	0	1 626	0.60	28
Boophilus decoloratus	88 620	43 029	15 148	7 353 (95)	154 150	56.85	63
Ixodes sp.	0	8	0	0	8	0.003	1
Rhipicephalus appendiculatus	3 298	1 387	737	355	5 777	2.13	53
Rhipicephalus evertsi evertsi	7 328	1 338	109	43	8 818	3.25	61
Rhipicephalus simus	16	0	0	0	16	0.006	1
Rhipicephalus zambeziensis	26 342	7 112	1 415	606	35 475	13.08	60
Lice	Nymphs		Adults				
Damalinia aepycerus	7 448		2 780		10 228	18.57	47
Damalinia elongata	22 188		11 928		34 116	61.94	47
Linognathus aepycerus	3 896		2 356		6 252	11.35	49
Linognathus nevilli	2 440		1 184		3 624	6.58	27
Linognathus sp.	428		428		856	1.55	18
Louse flies	Adults						
Hippobosca fulva	50				50	90.91	19
Lipoptena paradoxa	5				5	9.09	4

( ) = Number of maturing *B. decoloratus* females, i.e. idiosoma > 4.0 mm in length

TABLE 4 Arthropod parasites collected during 1980/81 from 60 impalas in the Biyamiti region, Kruger National Park

Arthropod species	Number of arthropods collected				Total	Proportional abundance %	No. of impalas infested
Ixodid ticks	Larvae	Nymphs	Males	Females			
Amblyomma hebraeum	27 225	3 559	25	4	30 813	10.56	60
Amblyomma marmoreum	159	0	0	0	159	0.05	8
Boophilus decoloratus	126 952	50 692	18 276	8 724 (134)	204 644	70.13	60
Haemaphysalis aciculifer	16	0	0	0	16	0.005	1
Rhipicephalus appendiculatus	9 393	5 892	225	151	15 661	5.37	54
Rhipicephalus evertsi evertsi	26 628	3 865	81	35	30 609	10.49	59
Rhipicephalus simus	0	0	1	0	1	0.0003	1
Rhipicephalus zambeziensis	7 575	1 889	303	123	9 890	3.39	54
Lice	Nymphs		Adults				
Damalinia aepycerus	1 328		944		2 272	21.02	37
Damalinia elongata	340		412		752	6.96	17
Linognathus aepycerus	2 164		1 568		3 732	34.53	37
Linognathus nevilli	2 388		1 252		3 640	33.68	34
Linognathus sp.	240		172		412	3.81	11
Louse flies	Adults						
Hippobosca fulva	117				117	97.50	18
Lipoptena paradoxa	3				3	2.50	1

( ) = Number of maturing *B. decoloratus* females, i.e. idiosoma > 4.0 mm in length

TABLE 5 Arthropod parasites collected during 1992/93 from 45 yearling impala males at Skukuza, Kruger National Park

Arthropod species	Number of arthropods collected				Total	Proportional abundance %	No. of impalas infested
Ixodid ticks	Larvae	Nymphs	Males	Females			
Amblyomma hebraeum	5 076	1 070	8	0	6 154	25.05	45
Amblyomma marmoreum	340	0	0	0	340	1.38	22
Boophilus decoloratus	4 678	3 792	1 619	1 164 (20)	11 253	45.80	45
Hyalomma truncatum	2	0	0	0	2	0.01	1
Rhipicephalus appendiculatus	12	4	96	46	158	0.64	18
Rhipicephalus evertsi evertsi	410	92	20	12	534	2.17	34
Rhipicephalus zambeziensis	3 840	936	942	412	6 130	24.95	40
Lice*	Nymphs		Adults				
Damalinia aepycerus	1 750		1 131		2 881	22.75	41
Damalinia elongata	2 707		4 237		6 944	54.83	29
Linognathus aepycerus	1 195		1 102		2 297	18.14	39
Linognathus nevilli	271		130		401	3.17	18
Linognathus sp.	66		75		141	1.11	16

* = Only 42 animals examined for lice

( ) = Number of maturing *B. decoloratus* females, i.e. idiosoma > 4.0 mm in length

TABLE 6 Arthropod parasites collected during 1980/81 from 12 adult male impalas at Crocodile Bridge, Kruger National Park

Arthropod species	Number of arthropods collected				Total	Proportional abundance %	No. of impalas infested
Ixodid ticks	Larvae	Nymphs	Males	Females			
Amblyomma hebraeum	9 679	1 811	9	2	11 501	21.49	12
Amblyomma marmoreum	77	0	0	0	77	0.14	2
Boophilus decoloratus	11 040	8 260	4 300	1 947 (126)	25 547	47.74	12
Rhipicephalus appendiculatus	10 420	1 888	286	265	12 859	24.03	–
Rhipicephalus evertsi evertsi	1 664	314	61	18	2 057	3.84	12
Rhipicephalus simus	0	0	1	0	1	0.002	1
Rhipicephalus zambeziensis	1 408	48	11	7	1 474	2.75	8
Lice	Nymphs		Adults				
Damalinia aepycerus	96		72		168	10.05	4
Damalinia elongata	552		232		784	46.89	5
Linognathus aepycerus	524		192		716	42.82	6
Linognathus nevilli	4		0		4	0.24	1
Louse flies	Adults						
Hippobosca fulva	4				4	100.00	2

( ) = Number of maturing *B. decoloratus* females, i.e. idiosoma > 4.0 mm in length

TABLE 7 Arthropod parasites collected during the 1982 drought from ten drought-affected "terminal" impalas at Skukuza, Kruger National Park

Arthropod species	Number of arthropods collected				Total	No. of impalas infested
Ixodid ticks	Larvae	Nymphs	Males	Females		
Amblyomma hebraeum	5 715	853	99	49	6 716	10
Amblyomma marmoreum	27	2	0	0	29	4
Boophilus decoloratus	34 964	16 437	8 354	4 967 (60)	64 722	10
Ixodes sp.	1	0	0	0	1	1
Rhipicephalus appendiculatus	56	48	15	21	140	8
Rhipicephalus evertsi evertsi	2 224	264	51	28	2 567	9
Rhipicephalus zambeziensis	80	315	41	48	484	10
Lice	Nymphs		Adults			
Damalinia aepycerus	272		517		789	9
Damalinia elongata	3 896		2 008		5 904	4
Linognathus aepycerus	7 582		8 359		15 941	9
Linognathus nevilli	552		265		817	6
Linognathus sp.	1 264		520		1 784	4
Louse flies	Adults					
Lipoptena paradoxa	4				4	2

( ) = Number of maturing *B. decoloratus* females, i.e. idiosoma > 4.0 mm in length

TABLE 8 Arthropod parasites collected during the 1982 drought from 14 apparently healthy impalas at Skukuza, Kruger National Park

Arthropod species	Number of arthropods collected				Total	No. of impalas infested
Ixodid ticks	Larvae	Nymphs	Males	Females		
Amblyomma hebraeum	11 127	1 160	35	6	12 328	14
Boophilus decoloratus	19 597	16 051	6 307	3 168 (43)	45 123	14
Ixodes sp.	0	17	0	0	17	2
Rhipicephalus appendiculatus	4	120	18	8	150	10
Rhipicephalus evertsi evertsi	1 393	260	16	13	1 682	14
Rhipicephalus zambeziensis	5	180	18	22	225	9
Lice	Nymphs		Adults			
Damalinia aepycerus	233		723		956	14
Damalinia elongata	266		558		824	7
Linognathus aepycerus	1 389		2 282		3 671	13
Linognathus nevilli	48		152		200	5
Linognathus sp.	90		216		306	7
Louse flies	Adults					
Hippobosca fulva	2				2	1
Lipoptena paradoxa	5				5	3

( ) = Number of maturing *B. decoloratus* females i.e. idiosoma > 4.0 mm in length

TABLE 9 Arthropod parasites collected during 1980 from an impala lamb, yearling and adult male, and adult female at Pafuri, Kruger National Park

Arthropod species	Number of arthropods collected				Total	No. of impalas infested
Ixodid ticks	Larvae	Nymphs	Males	Females		
Amblyomma hebraeum	1 105	196	0	0	1 301	4
Amblyomma marmoreum	11	0	0	0	11	1
Boophilus decoloratus	3 252	736	301	82	4 371	4
Rhipicephalus appendiculatus	3 832	2 280	1	1	6 114	4
Rhipicephalus evertsi evertsi	88	40	0	1	129	3
Rhipicephalus kochi	32	80	0	0	112	4
Rhipicephalus pravus group	8	0	0	0	8	1
Rhipicephalus zambeziensis	116	0	0	0	116	3
Lice	Nymphs		Adults			
Damalinia elongata	28		36		64	4
Linognathus aepycerus	16		0		16	1
Linognathus nevilli	432		168		600	4

TABLE 10 Arthropod parasites collected during 1992/93 from 21 yearling impala males at Pafuri, Kruger National Park

Arthropod species	Number of arthropods collected				Total	Proportional abundance %	No. of impalas infested
Ixodid ticks	Larvae	Nymphs	Males	Females			
Amblyomma hebraeum	440	308	4	0	752	6.31	17
Amblyomma marmoreum	8	0	0	0	8	0.07	2
Amblyomma tholloni	0	6	0	0	6	0.05	2
Boophilus decoloratus	1 842	1 982	1 032	712 (52)	5 568	46.75	21
Rhipicephalus appendiculatus	1 076	756	30	22	1 884	15.82	13
Rhipicephalus evertsi evertsi	464	112	28	2	606	5.09	20
Rhipicephalus kochi	1 884	416	118	32	2 450	20.57	17
Rhipicephalus zambeziensis	266	54	190	126	636	5.34	16
Lice	Nymphs		Adults				
Damalinia aepycerus	624		264		888	18.93	15
Damalinia elongata	0		2		2	0.04	1
Linognathus aepycerus	2 072		986		3 058	65.20	19
Linognathus nevilli	482		190		672	14.33	14
Linognathus sp.	40		30		70	1.49	5

( ) = Number of maturing *B. decoloratus* females i.e. idiosoma > 4.0 mm in length

at the same time ($P = 0.065$) (Table 11), but when the 1980 impalas were included, the differences among the groups were marginal ($P = 0.11$).

The apparent differences in the effects of drought on tick burdens may result from differences in the timing of the collections in relation to rainfall. The collections in 1992/93 began in March 1992. They were made in a year of above average rainfall following 2 years of below average rainfall at the end of a dry cycle, with particularly low rainfall during the summer of 1991/92. There was a marked reduction in the number of questing ticks collected by drag-sampling at Skukuza in 1992/93 (Horak, De Vos & Braack 1995b). This probably resulted from a reduction in the number of hosts and a loss of habitat for free-living ticks. Only 1 000 impalas were counted in the 1992 game counts, a quarter of the average count for other years, and there was a decrease in the amount of standing vegetation and loss of the grass mat which provide habitat for the free-living stages of ticks (Horak *et al.* 1995b). The 1982 collections were made in November and early December, at the beginning of the 1982/83 drought. The collections followed an extended period of low rainfall beginning in February 1982. However, this drought occurred at the end of the wet cycle of the 1970s (Whyte & Joubert 1988), and was preceded by 2 years of average to above average rainfall and impala populations (Horak *et al.* 1995b). There were no collections of questing ticks in 1982 but the numbers were probably higher than in 1992. The higher total tick burden on the "terminal" impalas in 1982 is similar to the observation that impalas in poor condition in the spring in the Mlawula-Mbuluzi-Simunye Nature Reserve complex in Swaziland were more heavily infested than those in better condition (Gallivan *et al.* 1995).

The seasonal patterns of infestation were similar in the three southern locations. The total tick burdens of the impalas examined at Skukuza and in the Biyamiti region during 1980/81 were lowest in the summer and highest in the late winter and spring ($P < 0.001$), with a secondary peak in April (Fig. 2). The late winter/spring peak coincides with the hatch and subsequent availability of *B. decoloratus* larvae, and the April peak coincides with the availability of *R. appendiculatus* and *R. zambeziensis* larvae. There was a significant month x location interaction ($P = 0.002$) caused by higher burdens at Skukuza from January to June 1980, and higher burdens in the Biyamiti region from July 1980 to January 1981. The higher burdens at Skukuza were caused by the higher intensity of infestation of *R. zambeziensis* larvae, while the higher burdens in the Biyamiti region were caused by the higher intensity of infestation of *B. decoloratus*.

TABLE 11 Mean intensities of infestations of arthropods on impalas during the 1982 and 1992 droughts in the Kruger National Park compared to animals examined during 1980/81

Arthropod species	Stage of development	1982			1992	
		"Terminal" (n = 10)	Healthy (n = 14)	1980 (n = 14)	1980/81 (n = 41)	1992/93 (n = 45)
Ixodid ticks						
Amblyomma hebraeum	Larvae	571.5	794.8	1 023.5	892.6	112.8
	Nymphs	85.3	82.9	138.4	138.3	23.8
	Adults	14.8	2.9	0.8	1.1	0.2
Amblyomma marmoreum	Larvae	2.7	0	13.6	29.9	7.6
Boophilus decoloratus	All	6 472.2	3 223.1	3 161.1	2 641.6	250.1
Rhipicephalus appendiculatus	Larvae	5.6	0.3	5.7	40.1	0.3
	Nymphs	4.8	8.6	1.1	23.1	0.1
	Adults	3.6	1.9	0.8	18.8	3.1
Rhipicephalus evertsi evertsi	Immatures	248.8	118.1	155.4	141.9	11.2
	Adults	7.9	2.1	3.0	2.8	0.7
Rhipicephalus zambeziensis	Larvae	8.0	0.4	0.0	342.5	85.3
	Nymphs	31.5	12.9	44.0	90.2	20.8
	Adults	8.9	2.9	2.1	37.3	30.1
Total ixodid ticks		7 492.7	4 251.8	4 549.6	4 400.9	546.0
Lice					*	*
Damalinia aepycerus	Nymphs, adults	78.9	68.3	108.0	249.3	70.2
Damalinia elongata	Nymphs, adults	590.4	58.9	207.4	1 029.3	175.0
Linognathus aepycerus	Nymphs, adults	1 594.1	262.2	89.7	97.5	58.5
Linognathus nevilli	Nymphs, adults	81.7	14.3	46.9	77.7	10.1
Linognathus sp.	Nymphs, adults	178.4	21.9	22.3	23.2	3.3
Total lice		2 523.5	425.5	474.3	1 477.1	317.2

* For lice n = 21 in 1980/81 and 39 in 1992/93

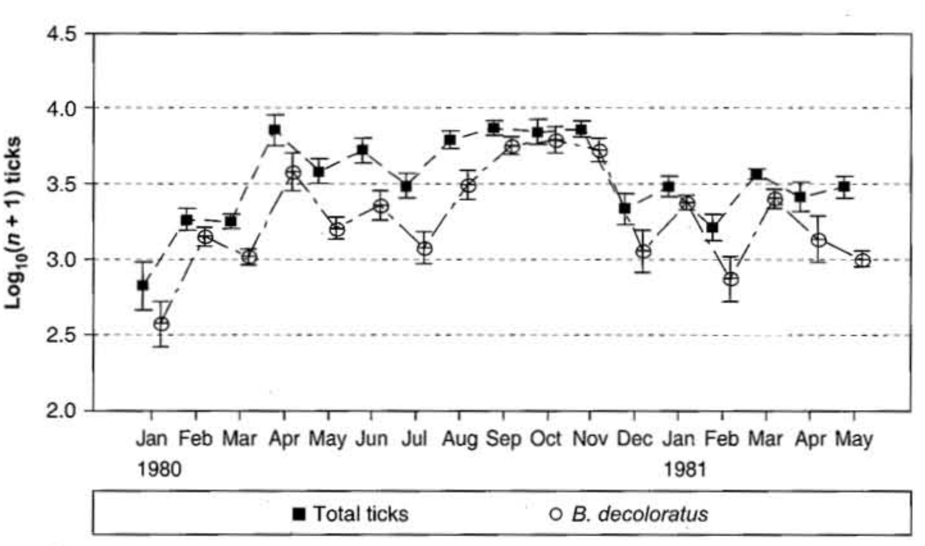

FIG. 2

Seasonal pattern of the total tick burden and intensity of infestation of all life stages of *Boophilus decoloratus* (x ± 1SE) on impalas at Skukuza and in the Biyamiti region in 1980/81. No lambs were collected after January 1981 and no yearlings after February 1981. The monthly sample at each locality ranged from two to six or seven impalas

The seasonal pattern at Skukuza was similar in 1980/81 and 1992/93. However, there was a significant month x location interaction (P = 0.004) between Skukuza and Pafuri in 1992/93. Burdens were significantly higher (P < 0.05) at Skukuza in the spring and summer, and tended to be higher at Pafuri in the autumn and winter, although the latter differences were not statistically significant (P > 0.05). The higher tick burdens at Pafuri corresponded to periods with the highest intensity of infestation of *B. decoloratus* and *R. kochi* at this location, and the higher burdens at Skukuza corresponded with the peak activity period of *B. decoloratus* at the southern locations in the KNP.

The total tick burdens during 1980/81 at Skukuza and in the Biyamiti region were significantly lower on lambs than on yearlings and adults (P = 0.004), with significant month x age (P = 0.001) and location x age (P = 0.005) interactions. The age x month interaction was caused by low burdens on newborn lambs relative to yearlings and adults in December, and higher burdens on yearlings in April, June and October. The location x age interaction resulted from high burdens on yearlings at Skukuza compared to those on yearlings in the Biyamiti region, and on lambs and adults at Skukuza. The intensity of infestation on lambs and adults did not differ between Skukuza and the Biyamiti region, and there was no difference between the age classes in the latter region. The total tick burdens of the adult male and female impalas did not differ significantly (P = 0.38).

Amblyomma hebraeum

Adult *A. hebraeum* prefer large herbivores as hosts, whereas the immature stages feed on these animals and on a variety of smaller herbivores, leporids and ground-nesting birds (Theiler 1962; Norval 1983; Horak, MacIvor, Petney & De Vos 1987). Impalas, which we consider to be medium-sized herbivores, are excellent hosts of the immature stages and harbour virtually identical burdens to those of greater kudus in the KNP (Horak *et al.* 1992; Horak 1998).

All the impalas were infested with *A. hebraeum* larvae and nymphs in 1980/81. The intensity of infestation of both stages was higher at Skukuza and Crocodile Bridge than in the Biyamiti region ($P \leq$ 0.001), but the intensity of infestation did not differ significantly among Skukuza, Biyamiti and Pafuri in July 1980 (P = 0.14). All the yearling males were infested with nymphs and 96 % were infested with larvae at Skukuza in 1992/93, but the intensities of infestations of both stages were significantly lower (P < 0.001) than in 1980/81, reflecting the low number of questing larvae in 1992/93 (Horak *et al.* 1995b). Only 67 % of the yearling males collected at Pafuri during 1992/93 were infested with larvae, and the same percentage with nymphs. The prevalence and intensities of infestation of both stages were lower at Pafuri than at Skukuza ($P \leq$ 0.006). This corresponds with observations on scrub hares, *Lepus saxatilis* (Horak, Spickett, Braack & Penzhorn 1993), that the intensity of infestation of *A. hebraeum* was lower in the north of the KNP.

While impalas appear to be good hosts for the immature stages, they are poor hosts for adult *A. hebraeum*. The prevalence of adults was 31.7 % in 1980/81, and did not differ among locations ($P \geq$ 0.19). The largest infestation was seven ticks, with 33 of the 44 infested impalas only harbouring one or two ticks. At Skukuza the prevalence of *A. hebraeum* adults was significantly higher (P < 0.001) in 1980/81 (46 %) than in 1992/93 (9 %), but the prevalence of adults did not differ between Skukuza and Pafuri in 1992/93. The maximum infestation in 1992/93 was two ticks, and no females were collected.

The intensity of infestation of *A. hebraeum* larvae varied significantly by month (P < 0.001) at Skukuza and in the Biyamiti region in 1980/81. There appeared to be two peaks of infestation, one from April to June, and the other during November and December (Fig. 3). The intensity of infestation was significantly higher at Skukuza than in the Biyamiti region from June to August (P < 0.05). The seasonal patterns of *A. hebraeum* larvae did not differ significantly (P > 0.18) between Skukuza and Crocodile Bridge, or between 1980/81 and 1992/93 at Skukuza. The seasonal pattern was similar at Skukuza and Pafuri from March to August 1992, but the intensity of infestation increased at Skukuza in October 1992 and declined at Pafuri. The intensity of infestation remained lower at Pafuri through April 1993. The intensity of infestation of *A. hebraeum* nymphs was significantly higher (P < 0.001) in late winter than in the summer. The seasonal patterns of occurrence of nymphs were similar at Skukuza in 1980/81 and 1992/93, and at Skukuza and Pafuri in 1992/93. The prevalence of adults did not differ seasonally in any of the collections (P > 0.2).

In earlier surveys in the KNP there was no clear pattern of seasonal abundance of the immature stages of *A. hebraeum* on greater kudus, scrub hares and helmeted guineafowls, *Numida meleagris* (Horak, Spickett, Braack & Williams 1991; Horak

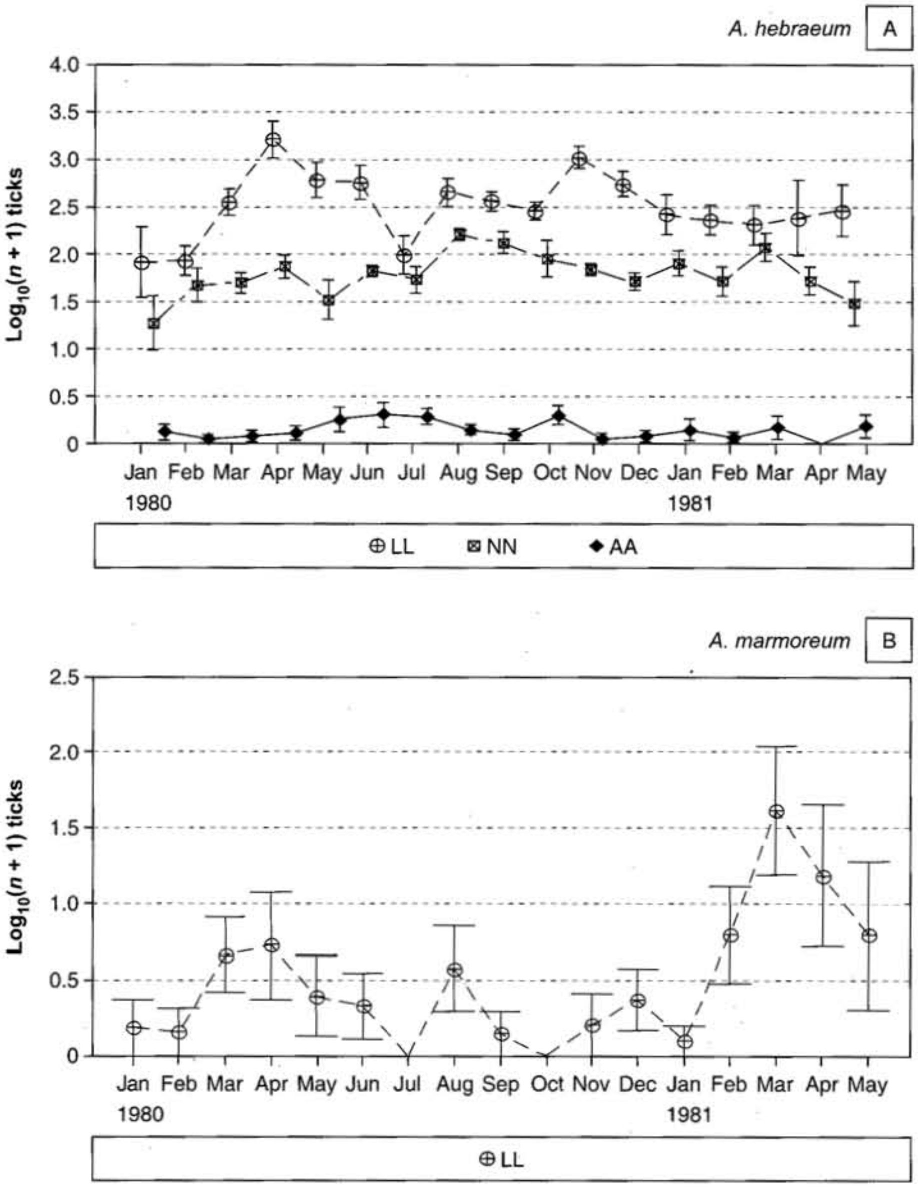

FIG. 3 Seasonal pattern of the intensity of infestation of [A] all life stages of *Amblyomma hebraeum* (x ± 1SE), and [B] larvae of *Amblyomma marmoreum* (x ± 1SE) on impalas at Skukuza and in the Biyamiti region during 1980/81. No lambs were collected after January 1981 and no yearlings after February 1981. The monthly sample at each locality ranged from two to six or seven impalas

et al. 1992; 1993). There were apparent peaks on warthogs, *Phacochoerus africanus* (Horak, Boomker, De Vos & Potgieter 1988b), and Burchell's zebras, *Equus burchellii* (Horak, De Vos & De Klerk 1984), but these seasonal patterns differ from those observed on impalas. The apparent seasonal patterns on some host species may be a function of the animals selected in the survey rather than the number of questing ticks as there does not appear to be a seasonal pattern in the number of questing *A. hebraeum* larvae (Spickett, Horak, Van Niekerk & Braack 1992).

The intensity of infestation of *A. hebraeum* larvae did not differ significantly among age classes ($P = 0.20$), but the intensity of infestation of nymphs was significantly higher on yearlings and adult impalas than on lambs ($P < 0.001$). The prevalence of adults was also significantly higher ($P = 0.017$) on yearlings (40 %) and adults (43 %) than on lambs (11.5 %). The intensities of infestations of larvae and nymphs did not differ significantly between the sexes in the adult animals ($P \geq 0.88$), but the prevalence of *A. hebraeum* adults was significantly higher ($P = 0.02$) on adult males (54 %) than on adult females (26 %). The higher prevalence and intensity of infestation of *A. hebraeum* adults on adult animals, and on adult males in particular, are consistent with the patterns reported for impalas in Swaziland (Gallivan *et al.* 1995) and kudus in the KNP (Horak *et al.* 1992).

The intensities of infestations of *A. hebraeum* larvae and nymphs did not differ significantly among the impalas examined at Skukuza in 1980 and those examined at the same locality during the 1982 drought. However, both the prevalence (100 %) and intensity of infestation of adults were significantly higher ($P < 0.002$) on the "terminal" impalas in 1982 than on the apparently healthy animals and on the impalas examined in 1980. In Swaziland, impalas infested with *A. hebraeum* adults were in poorer condition than uninfested animals, and the highest intensities of infestation with adult ticks were on adult males at the end of the dry season and after mating, periods in which these animals were already in poor condition (Gallivan *et al.* 1995). This suggests that the infestation may be secondary to the loss of resistance in stressed animals rather than a primary effect.

Amblyomma marmoreum

Amblyomma marmoreum prefers tortoises as hosts in all its stages of development (Norval 1975; Dower, Petney & Horak 1988), but the immature stages will feed on other reptiles and the larvae will also feed on carnivores, herbivores, leporids and ground-nesting birds (Norval 1975; Horak *et al.* 1987). In 1980/81, 37.6 % of the impalas were infested with *A. marmoreum* larvae. The prevalence was lower than that on helmeted guineafowls and scrub hares, but higher than on kudus examined in the KNP (Horak *et al.* 1991; 1992; 1993).

The intensity of infestation of *A. marmoreum* larvae on impalas ranged from 4–235, but 71 % of the infested animals harboured fewer than 50 larvae. The prevalence was significantly higher ($P = 0.001$) at Skukuza (34.6 %) than in the Biyamiti region (8.0 %). However, it did not differ among adult males at Skukuza, Crocodile Bridge and the Biyamiti region. This apparent contradiction occurred because the prevalences of *A. marmoreum* larvae on lambs and yearlings were much higher at Skukuza (50 %) than in the Biyamiti region (8 %) while the prevalence on adult impalas did not differ significantly between the two areas ($P = 0.24$). The prevalence at Skukuza did not differ significantly between 1980/81 and 1992/93, but the intensity of infestation was marginally higher in 1980/81 than in 1992/93 ($P = 0.07$). Prevalence at Skukuza in 1992/93 (48 %) was significantly higher ($P = 0.004$) than at Pafuri (9.5 %). This is similar to the differences recorded on scrub hares at Skukuza and in the north of the KNP (Horak *et al.* 1993). Only two impalas, both at Skukuza in 1981, were infested with *A. marmoreum* nymphs.

The prevalence and intensity of infestation of *A. marmoreum* larvae did not differ significantly ($P \geq 0.25$) on impalas at Skukuza and in the Biyamiti region from January 1980 to January 1981. However, the intensity of infestation was higher from February to May 1981 (Fig. 3). The pattern was similar in the 1992/93 ($P = 0.51$) samples where the intensity of infestation was higher in March and April in 1993 than in 1992. The higher larval burdens from March to May reflect the seasonal pattern of questing larvae on the vegetation in the park during these months (Spickett *et al.* 1992), and are similar to the patterns recorded on helmeted guineafowls, greater kudus and scrub hares in the KNP (Horak *et al.* 1991; 1992; 1993).

The prevalence and intensity of infestation of *A. marmoreum* larvae did not differ significantly among age classes ($P \geq 0.10$), or between sexes in the adult impalas ($P = 0.97$). The intensity of infestation of *A. marmoreum* larvae was higher on the "terminal" impalas in the 1982 drought at Skukuza than on the apparently healthy animals ($P = 0.05$). It was also marginally higher ($P = 0.08$) on the impalas examined in 1980 than on the apparently healthy animals in 1982.

Amblyomma tholloni

African elephants, *Loxodonta africana*, are the preferred hosts of all stages of *A. tholloni*, but the immature stages will also infest birds, reptiles, other wild mammals, and domestic cattle, sheep and goats (Theiler 1962; Norval 1983; Walker 1991). The recovery of nymphs from two impalas at Pafuri must be viewed as accidental infestations in a habitat in which there are many elephants.

Boophilus decoloratus

All the impalas were infested with *B. decoloratus*. Considering their relatively small size, impalas are remarkably good hosts of this tick as the burdens in the Biyamiti region were similar to those on greater kudus in the same region (Horak *et al.* 1992; Horak 1998). *Boophilus decoloratus* accounted for 5.6–98.6 % (mean = 57.8 %) of the total tick burden on individual impalas, and also accounted for most of the tick burden on blue wildebeest, *Connochaetes taurinus*, Burchell's zebras and greater kudus in the KNP (Horak *et al.* 1983b; 1984; 1992). However, questing larvae of *B. decoloratus* are not the most abundant species on the vegetation in the Crocodile Bridge region or at Skukuza (Spickett *et al.* 1992; Horak *et al.* 1995b; Spickett, Horak, Heyne & Braack 1995; Horak 1998), even though it was the most common tick on impalas at both localities (Table 2). Its predominance on host animals is probably because it is present throughout the year in the KNP, infests a wide range of medium to large-size ungulates, and, because it is a one-host tick, survival from one developmental stage to the next is high (Baker & Ducasse 1967; Mason & Norval 1980; Horak *et al.* 1983a; 1984; 1992).

The one-host life cycle strategy of *B. decoloratus* reduces the losses between developmental stages that occur in the multi-host ticks during their moults off the host. The mean ratio of *B. decoloratus* larvae to nymphs to adults on all the impalas examined in the KNP was 3.49:1.69:0.00, and the ratio of males to females 1.97:1.00. These ratios imply a very satisfactory transition from one developmental stage to the next on impalas. Colborne (1989) recorded a ratio of 2.31:1.31:1.00 for larvae to nymphs to adults and a ratio of males to females of 1.89:1.00 on impalas in the south-eastern lowveld of Zimbabwe. The ratio of larvae to nymphs to adults on impalas is also within the range recorded on Burchell's zebras, bushbuck, *Tragelaphus scriptus* and greater kudus in the KNP (Horak *et al.* 1983a; 1984; 1992).

In 1980/81 the intensity of infestation was higher and *B. decoloratus* accounted for a greater proportion of the tick burden in the Biyamiti region than at Skukuza ($P \leq 0.001$). At Skukuza the intensity of infestation was lower in 1992/93 than in 1980/81, and *B. decoloratus* accounted for a lower proportion of the total tick burden ($P < 0.001$). The intensity of infestation did not differ significantly between Skukuza and Pafuri in 1992/93, but *B. decoloratus* accounted for a higher proportion of the total tick burden at Pafuri ($P = 0.001$). (The latter observation appears to contradict the data in the tables. However, the tabulated data summarize all of the ticks collected, whereas this compares the percentages on individual animals). The intensity of infestation was higher on adult males in the Biyamiti region than at Crocodile Bridge, and on impalas in the Biyamiti region than at Pafuri in July 1980, but the differences were not statistically significant ($P > 0.1$). *Boophilus decoloratus* accounted for a greater proportion of the total tick burden on adult males in the Biyamiti region than at Crocodile Bridge (69 % vs 50 %; $P = 0.003$), and in the Biyamiti region than at Pafuri in July, 1980 (55 % vs 36 %), although the latter difference was not statistically significant.

The differences in the intensity of infestation of *B. decoloratus* and its proportion of the total tick burden among regions and between years may result from a number of factors, particularly climate and host availability. There appears to be a close association between the number of questing *B. decoloratus* larvae and rainfall during the preceding year at Skukuza (Horak *et al.* 1995b), and in the present study, the intensity of infestation of *B. decoloratus* appears to be higher in regions where *R. appendiculatus* predominates over *R. zambeziensis*, a tick normally found in drier areas (Norval, Walker & Colborne 1982). In addition, the availability of hosts may play an important role as exemplified by the decrease in the number of questing *B. decoloratus* larvae at Skukuza in 1992/93 following the decline in the impala population in 1992.

The seasonal patterns in the intensity of infestation of *B. decoloratus* on impalas were similar in the three southern locations. In 1980/81 the intensity was lowest in the summer and highest in the spring at Skukuza and in the Biyamiti region ($P < 0.001$; Fig. 2). *Boophilus decoloratus* accounted for the highest proportion of the total tick burden in the spring and early summer, and the lowest proportion in the late autumn and winter ($P < 0.001$). The intensity of infestation did not differ between Skukuza and the Biyamiti region in the autumn and winter, but was significantly higher in the Biyamiti region during the winter and spring. *Boophilus decoloratus* accounted for a greater proportion of the tick burden in the Biyamiti region than at Skukuza during July and August, and November and December ($P < 0.05$). The seasonal pattern was similar at Skukuza in 1980/81 and 1992/93, but *B. decoloratus* accounted for a greater proportion of the tick burden from March to September in 1980 than in 1992. The proportion was similar from October 1980 to April 1981 and from October 1992 to April 1993. In 1992/1993, the intensity of infestation was higher at Pafuri from March to August 1992, and higher at Skukuza from October 1992 to April 1993 ($P = 0.002$). Peak intensity of infestation occurred in August at Pafuri and in October at Skukuza.

The seasonal pattern in the intensity of infestation of *B. decoloratus* on impalas is similar to that on blue wildebeest, Burchell's zebras and greater kudus in the KNP (Horak *et al.* 1983b; 1984; 1992). The pre-hatch period of *B. decoloratus* eggs is longer in the cooler winter months than in the warmer months, and eggs laid in the winter hatch synchronously with those produced at higher temperatures in the spring (Robertson 1981; Spickett & Heyne 1990). The synchronous hatch and extended period of larval survival during the winter (Spickett & Heyne 1990) result in an increase in the number of questing free-living *B. decoloratus* larvae on the vegetation in the southern KNP from August to November (Spickett *et al.* 1992; Horak, Spickett & Braack 2000a). Impalas may also have a reduced resistance to tick infestation at this time because they are on a lower plane of nutrition during the dry winter season and are in poorer condition (Gallivan *et al.* 1995), which reduces their resistance to tick infestation. The higher burdens in the autumn and winter at Pafuri, and the peak in infestation during August, may be due to the 2 °C higher average winter temperature there, resulting in earlier hatching of larvae than at Skukuza.

The intensity of infestation of *B. decoloratus* was highest on yearlings and lowest on lambs ($P <$ 0.001) at Skukuza and in the Biyamiti region during 1980/81. This was caused by the low intensity of infestation on newborn lambs in December and the high intensity on yearlings in April. The intensity of infestation did not differ among the age classes in the other months. The intensities of infestations of all stages of *B. decoloratus* were significantly lower on lambs in December ($P < 0.01$) indicating that the low intensity did not occur simply because there was not sufficient time for the development of the nymph and adult stages. In the other months, the intensity of infestation of larvae was lower on adult impalas ($P = 0.004$) and the intensity of infestation of adult *B. decoloratus* was lower on lambs ($P =$ 0.003) while the intensity of infestation of nymphs was highest on yearlings ($P = 0.05$). The proportion of the total tick burden did not differ among the age classes ($P = 0.20$), except in December when it was significantly lower on lambs than on yearlings and adults ($P < 0.001$). The intensity of infestation and proportion of the total tick burden on adult impalas did not differ between the sexes ($P \geq 0.27$). The age/sex pattern in the distribution of *B. decoloratus* on impalas differs from that on kudus in the KNP on which there was no difference in the intensity of infestation between age classes (Horak *et al.* 1992). However, the intensity of infestation of adult *B. decoloratus* was higher on adult male kudus than on adult females. There was no difference in the intensities of infestations of any stage of development of *B. decoloratus* between the sexes of adult impalas.

The "terminal" impalas at Skukuza in the 1982 drought were more heavily infested with *B. decoloratus* than the apparently healthy animals examined at the same time or the animals examined in 1980. *Boophilus decoloratus* also accounted for a higher percentage of the total tick burden on the impalas in 1982 than in 1980 ($P = 0.002$). Comparing only the two groups of impalas examined in 1982, the percentage was marginally higher on the "terminal" animals than on the apparently healthy animals ($P = 0.07$). The collections in the 1982 drought were made during the period of peak infestations of *B. decoloratus*, and followed 2 years of above average rainfall. A reduction in resistance in impalas on a low plane of nutrition and the potentially high number of questing *B. decoloratus* larvae probably contributed to the higher burdens in 1982, particularly on the "terminal" animals.

Haemaphysalis aciculifer

The preferred hosts of the adults of this tick are wild bovids, on which it seldom occurs in large numbers (Walker 1991; Horak, Keep, Spickett & Boomker 1989). The immature stages parasitize rodents and ground-nesting birds (Horak & Boomker 1998). Since 1977 one of us (I.G.H.) has examined more than 1 200 animals belonging to many species in the KNP and has collected a total of only two male *H. aciculifer* from an eland, *Taurotragus oryx*, and 15 adults from a honey badger, *Mellivora capensis* (Horak *et al.* 1983a; Horak, Braack, Fourie & Walker 2000b), the collection of 16 larvae from a single impala must be viewed as an accidental infestation with a tick that is apparently rare in the KNP.

Hyalomma truncatum

Adult *H. truncatum* prefer large ungulates, and frequently those with thick skins as hosts (Walker 1991). This tick is abundant in the KNP judging by the large numbers of its immature stages collected from scrub hares (Horak *et al.* 1993; Horak, Spickett, Braack, Penzhorn, Bagnall & Uys 1995a), and the presence of adults on giraffes, *Giraffa camelopardalis*, and Burchell's zebras (Horak *et al.* 1983a; 1984). No adults were collected from the impalas confirming that they are not good hosts of this stage of development. The recovery of larvae from a single impala examined at Skukuza is unusual because the preferred hosts of the immature stages at this locality, and elsewhere, are scrub hares, bushveld gerbils, *Tatera leucogaster* and other rodents (Walker 1991; Horak *et al.* 1993; Braack, Horak, Jordaan, Segerman & Louw 1996).

Rhipicephalus appendiculatus

All stages of development of *R. appendiculatus* prefer the larger bovids as hosts (Yeoman & Walker 1967; Walker 1974; Norval *et al.*1982; Walker, Keirans & Horak 2000). Large numbers of adults have also been collected from lions, *Panthera leo*, in the KNP (Horak *et al.* 2000b). The immature stages are found on medium-sized and smaller antelope species, on carnivores and on hares, as well as on the larger bovids (Norval *et al.* 1982; Walker *et al.* 2000). The intensities of infestations of *R. appendiculatus* larvae and nymphs on impalas in the Biyamiti region were similar to those on greater kudus in the same area (Horak *et al.* 1992), but the intensity of infestation of *R. appendiculatus* adults was much higher on kudus.

Rhipicephalus appendiculatus larvae were present from March to October with a peak in April to June at Skukuza and in the Biyamiti region during 1980/81. Nymphs were present from March or April to December with a June to September peak, and adults were present from October to June with a February to March peak (Fig. 4). With minor differences, the seasonal patterns were similar in all locations, and were similar to those on greater kudus in the Biyamiti region (Horak *et al.* 1992) and on impalas in the Limpopo Province (Horak 1982) and in Swaziland (Gallivan & Surgeoner 1995). The seasonal patterns of *R. appendiculatus* larvae and adults were similar to their activity periods on the vegetation near Crocodile Bridge 8 to 10 years later (Spickett *et al.* 1992), but the peak activity period of the nymphs was later (August to January) on the vegetation. Although varying in intensity, *R. appendiculatus* adults were present throughout the year on the greater kudus, while their activity period appeared to be delayed on impalas in Swaziland. However, these differences, like the minor differences between locations in the present study, may reflect differences in microclimatic conditions and the spatial distributions of the hosts, two factors which influence the activity of *R. appendiculatus* (Minshull & Norval 1982).

The intensities of infestations of *R. appendiculatus* larvae and nymphs were higher in the Biyamiti region than at Skukuza during 1980/81 ($P = 0.005$ and $P < 0.001$ respectively), but the intensity of infestation of adults was higher at Skukuza ($P = 0.039$). The intensity of infestation of *R. appendiculatus* larvae was significantly higher on adult male impalas at Crocodile Bridge than at Skukuza and in the Biyamiti region ($P < 0.001$). The intensities of infestations of nymphs were higher at Crocodile Bridge and in the Biyamiti region than at Skukuza ($P = 0.008$), but the intensity of infestation of adults did not differ among the three locations ($P = 0.91$).

At Skukuza the prevalences of *R. appendiculatus* larvae, nymphs and adults on the impalas examined during 1992/93 (6.7 %, 4.4 % and 33.3 %, respectively) were significantly lower ($P = 0.02$) than in 1980/81 (48.8 %, 31.7 % and 61 %, respectively). Only four *R. appendiculatus* larvae and two nymphs were collected from each of the infested impala in 1992/93. The mean intensity of infestation of *R. appendiculatus* adults was also lower in 1992/93 than in 1980/81 ($P < 0.001$) and no adults were collected from June 1992 to January 1993. The reduction in 1992/93 may reflect both the lack of hosts (Horak *et al.* 1995b) and the reduced survival of all life stages of *R. appendiculatus* under dry conditions and reduced cover (Short, Floyd, Norval & Sutherst 1989).

The intensities of infestations of *R. appendiculatus* larvae and nymphs were higher at Pafuri and in the Biyamiti region than at Skukuza ($P = 0.04$ and 0.001, respectively) during July 1980. The prevalence of larvae was significantly higher at Pafuri ($P = 0.002$) in 1992/93, where larvae were collected in May and August 1992 and April 1993. Nymphs were present at Pafuri from May to October 1992 and in April 1993. The prevalence and intensity of infestation were higher at Pafuri than at Skukuza ($P = 0.022$ and $P < 0.001$ respectively). The prevalence of *R. appendiculatus* adults did not differ between the two locations ($P = 0.60$). The intensity of infestation was significantly higher ($P < 0.05$) at Skukuza in March 1992, but did not differ between the two locations in the other months. No adults were collected in October and December 1992.

The intensity of infestation of *R. appendiculatus* larvae did not differ among age classes ($P = 0.66$), but the intensities of infestations of nymphs and adults were higher on yearling and adult impalas than on lambs ($P = 0.001$). The intensity of infestation of larvae was higher on adult female impalas than on adult males ($P = 0.044$), whereas the intensity of infestation of the nymphs did not differ between the sexes ($P = 0.29$). The intensity of infestation of adults was higher on adult male impalas than on adult females ($P = 0.001$), particularly from March

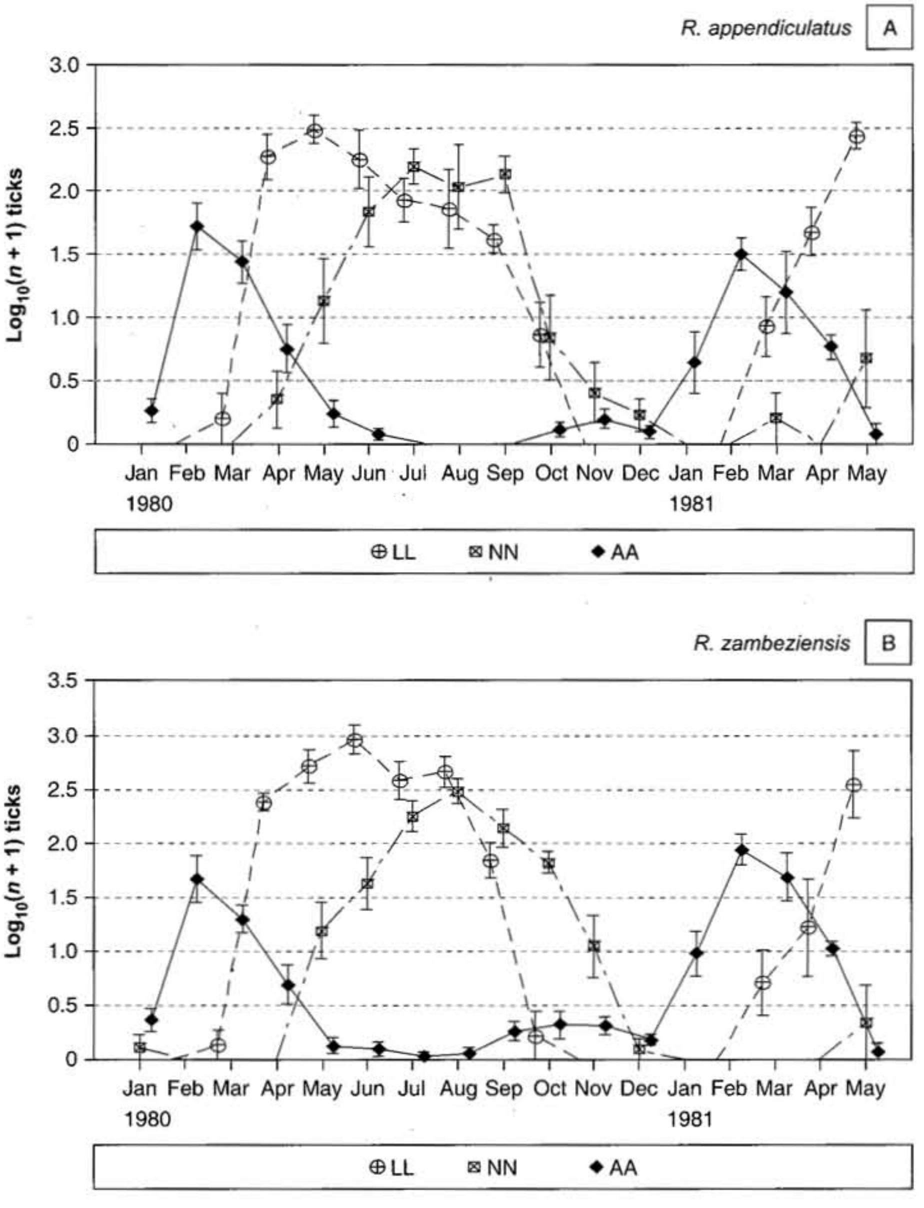

FIG. 4 Seasonal pattern of the intensity of infestation of [A] *Rhipicephalus appendiculatus* (x ± 1SE), and [B] *Rhipicephalus zambeziensis* (x ± 1SE) on impalas at Skukuza and in the Biyamiti region during 1980/81. No lambs were collected after January 1981 and no yearlings after February 1981. The monthly sample at each locality ranged from two to six or seven impalas

to May. The age/sex distribution of *R. appendiculatus* adults was similar to that reported for impalas in Swaziland (Gallivan *et al.* 1995). The low numbers of *R. appendiculatus* adults on lambs probably result from the higher allogrooming rates of lambs (Mooring & Hart 1992). Grooming would be effective in removing the adult ticks and nymphs, but possibly less so with the larvae. The peak activity of *R. appendiculatus* adults corresponds with the advent of breeding activity in impalas. Adult male impalas become less tolerant of other males several weeks prior to the rut, and territorial males do not tolerate other males (Murray 1982). This intolerance would reduce allogroomimg, and both auto- and allogrooming are reduced in territorial males (Mooring & Hart 1995), allowing an increase in the burden of adult ticks.

The intensities of infestations of *R. appendiculatus* larvae and nymphs did not differ among the two groups of impalas examined during the 1982 drought at Skukuza and those examined in 1980 (*P*

= 0.27 and 0.14, respectively), but the "terminal" impalas had a higher intensity of infestation of adults (P = 0.03) than the apparently healthy impalas in 1982 and the impalas examined in 1980.

Rhipicephalus evertsi evertsi

All stages of development of this two-host tick prefer equids and elands as hosts (Norval 1981). However, a large variety of herbivorous domestic and wild animals, including leporids, can serve as hosts for the immature stages (Walker *et al.* 2000). In 1980/81, 96.4 % of the impalas were infested with the immature stages of *R. evertsi evertsi*, and 64 % were infested with adults. The intensity of infestation of the immature stages was higher on impalas than on kudus in the Biyamiti region, but the intensity of infestation of adults was higher on kudus (Horak *et al.* 1992).

Horak (1982) reported a larvae to nymph ratio of 2.5:1.0 on impalas in the Limpopo Province, and Colborne (1989) reported a larvae to nymph ratio of 2.0:1.0 on impalas in south-eastern Zimbabwe. Colborne (1989) considered impalas to be good hosts of the immature stages of *R. evertsi evertsi* because of the high translation from one developmental stage to the next. These larvae to nymph ratios were similar to that on Burchell's zebras in the KNP (2.3:1.0), but higher than on Cape mountain zebras, *Equus zebra zebra*, in the Mountain Zebra National Park, Eastern Cape Province (1.3:1.0) (Horak *et al.* 1984; Horak, Knight & De Vos 1986a). Both these equid species are considered to be the preferred hosts of all stages of development of this tick (Walker *et al.* 2000). Excluding the impalas examined at Pafuri during July 1980, the ratio of *R. evertsi evertsi* larvae to nymphs on impalas in the KNP ranged from 4.1:1.0 to 8.4:1.0 (Tables 3–8, 10). The ratio on impalas in the Biyamiti region (6.9:1.0) was lower than the ratio of 9.6:1.0 on greater kudus (Horak *et al.* 1992), but still represents a poor translation from one developmental stage to the next, particularly as the moult takes place on the host.

The ratio of *R. evertsi evertsi* larvae to nymphs on impalas in the KNP was correlated with the intensity of infestation of *R. evertsi evertsi* larvae (r = 0.72; P = 0.066) and the total tick burden (r = 0.90; P = 0.005). Inclusion of the data from impalas in the Limpopo Province (Horak 1982) reduced the correlation between the larvae to nymph ratio and intensity of infestation of the larvae (r = 0.55; P = 0.16), but did not change the correlation between the larvae to nymph ratio and total tick burden (r = 0.91; P = 0.002). Rechav and co-workers (Clarke, Els, Heller-Haupt, Rechav & Varma 1989; Rechav, Dauth, Varma, Clarke, Els, Heller-Haupt & Dreyer 1989) have demonstrated an increase in serum globulin in the hosts and a reduction in the recovery and body weight of *R. evertsi evertsi* nymphs following successive challenges with larvae on guinea pigs and rabbits, suggesting that hosts develop immunity. However, there was a weak correlation between the intensity of infestation of *R. evertsi evertsi* larvae and the larvae to nymph ratio on impalas. Cross-resistance between tick species may explain the correlation between total tick burden and the ratio of *R. evertsi evertsi* larvae to nymphs on impalas. Cross-resistance has been demonstrated in laboratory and domestic animals, but a considerable variation in the degree of this resistance was reported in the studies (De Castro, Newsom & Herbert 1989).

During 1980/81 the intensity of infestation of the immature stages of *R. evertsi evertsi* at Skukuza and in the Biyamiti region varied significantly among months (P = 0.003). The lowest intensities of infestation were in January 1980 and 1981 (Fig. 5), and the highest intensities were in April and September 1980 and May 1981. However, there was considerable month-to-month variation throughout the remainder of the year, and the patterns were not consistent between the two locations. There was no seasonal pattern on adult male impalas at Crocodile Bridge, or on greater kudus in the Biyamiti region (Horak *et al.* 1992). On yearling male impalas at Skukuza in 1992/93, the lowest intensities were in April 1992 and February and March 1993, and the highest in May and October and November 1992. The prevalence of *R. evertsi evertsi* adults on impalas at Skukuza and in the Biyamiti region during 1980/81 was 100 % in April and May 1980, but did not differ significantly among months (P = 0.10). The intensity of infestation of adults was significantly higher in April 1980, but did not differ among the other months. There was no seasonal pattern in the infestation of *R. evertsi evertsi* adults on adult male impalas at Crocodile Bridge, on the yearling male impalas at Skukuza in 1992/92, or on greater kudus in the Biyamiti region.

Based on developmental periods obtained in the laboratory (Rechav, Knight & Norval 1977), *R. evertsi evertsi* can complete more than one life cycle per year at the temperatures prevailing in the KNP. There was no seasonal pattern for *R. evertsi evertsi* larvae questing on vegetation in the south of the KNP (Spickett *et al.* 1992), and the month-to-month variability in the number of questing larvae was

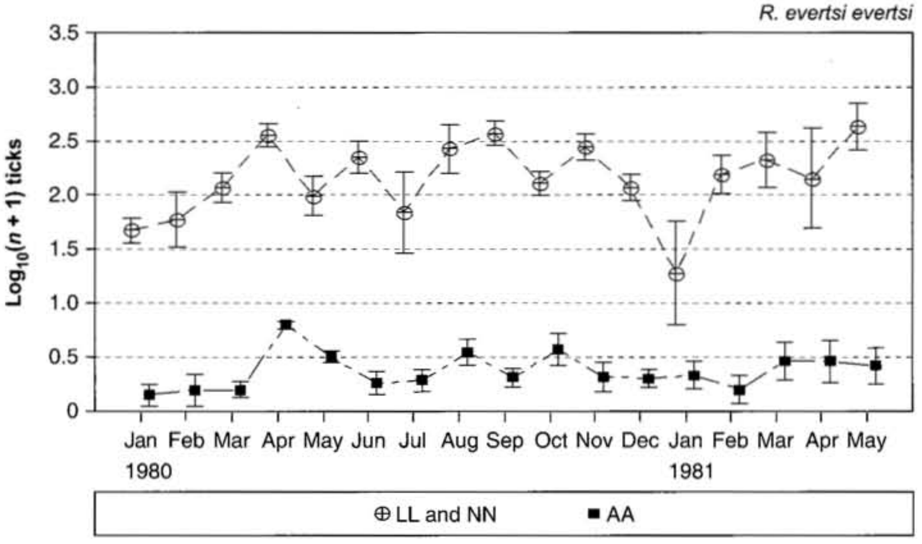

FIG. 5 Seasonal pattern of the intensity of infestation of *Rhipicephalus evertsi evertsi* (x ± 1SE) on impalas at Skukuza and in the Biyamiti region during 1980/81. No lambs were collected after January 1981 and no yearlings after February 1981. The monthly sample at each locality ranged from two to six or seven impalas

similar to the variability on impalas and kudus. The apparent peaks on impalas also differ from those on Burchell's zebras (Horak *et al.* 1984), one of the preferred hosts in the KNP. Based on the lack of a seasonal pattern and month-to-month variability in the number of questing larvae, the apparent seasonal patterns in the intensity of infestation of *R. evertsi evertsi* on impalas may simply reflect differences in the number of questing larvae and differences in the intensity of infestations among hosts.

The intensity of infestation of the immature stages of *R. evertsi evertsi* was higher in the Biyamiti region than at Skukuza in 1980/81 ($P < 0.001$), particularly during July and August, and was higher in the Biyamiti region than at Crocodile Bridge on adult male impalas ($P < 0.05$). The intensity of infestation was lowest at Pafuri in July 1980, but did not differ significantly among the three locations ($P = 0.09$). The prevalence and intensity of infestation of *R. evertsi evertsi* adults did not differ among the locations in 1980/81 ($P \leq 0.15$).

At Skukuza, the prevalences and intensities of infestations of the immature stages and adults of *R. evertsi evertsi* were significantly lower in 1992/93 than in 1980/81 ($P < 0.002$). The prevalence of the immature stages was higher ($P = 0.05$) on the yearling male impalas examined at Pafuri during 1992/93 (95.3 %) than on those at Skukuza (71 %). The intensity of infestation of the immature stages was also higher at Pafuri ($P = 0.022$), but the difference between the two locations was only significant in August 1992. The prevalence and intensity of infestation of adults did not differ significantly between the two locations 1992/93 ($P \geq 34$).

The intensity of infestation of the immature stages did not differ significantly among the age classes ($P = 0.42$), or between sexes of the adult impalas ($P = 0.72$). The prevalence of *R. evertsi evertsi* adults on adult impalas (76.5 %) was significantly higher ($P = 0.04$) than on lambs (50 %) and yearlings (56 %), and the intensity of infestation was significantly higher on adults than on lambs ($P = 0.013$). The prevalence and intensity of infestation with adult ticks did not differ between the sexes in adult animals ($P = 0.15$). These patterns are similar to those in Swaziland where the prevalence of *R. evertsi evertsi* nymphs did not differ among the age classes, the prevalence of adults was higher on adult and yearling impalas than on lambs, and the prevalence of adults did not differ between the sexes on adult impalas (Gallivan *et al.* 1995).

The intensity of infestation of the immature stages of *R. evertsi evertsi* did not differ significantly among the "terminal" impalas and the apparently healthy impalas in the 1982 drought at Skukuza and the impalas in 1980 ($P = 0.43$). The intenstity of infestation of adults was significantly higher on the "terminal" impalas than on the apparently healthy animals in 1982 ($P = 0.05$), but did not differ from the impalas examined in 1980 ($P > 0.20$).

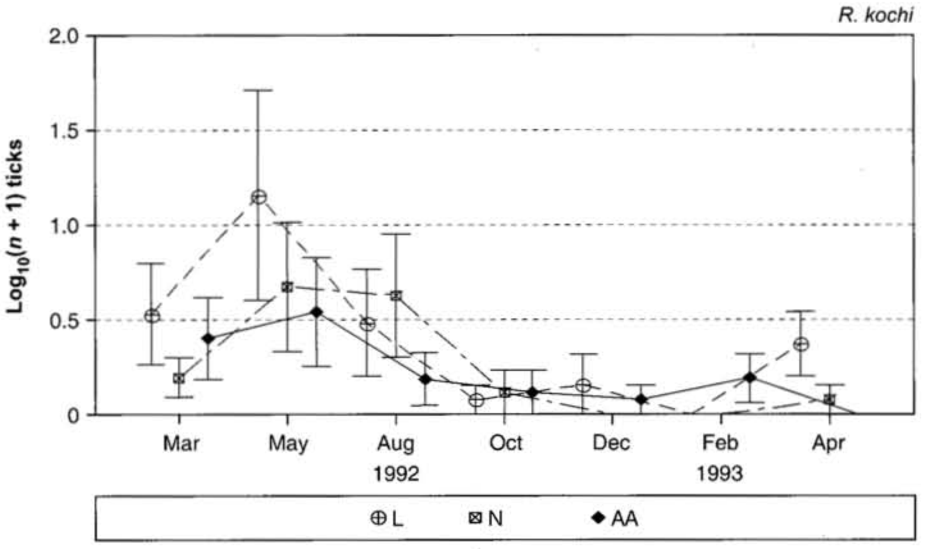

FIG. 6 Seasonal pattern of the intensity of infestation of *Rhipicephalus kochi* (x ± 1SE) on yearling male impalas at Pafuri during 1992/93. Three impalas were examined at 2–3 month intervals

Rhipicephalus kochi

Rhipicephalus kochi was only collected from impalas examined at Pafuri, and in South Africa it has been collected only in the far north-east of the Limpopo Province and of KwaZulu-Natal Province (Walker *et al.* 2000). The preferred hosts of all stages of development are medium-sized and larger antelopes and scrub hares (Walker *et al.* 2000). The prevalence and intensities of infestation of *R. kochi* larvae and nymphs were significantly higher ($P < 0.05$) from March to August 1992 than from October 1992 to February 1993 (Fig. 6). The prevalence and intensity of infestation of adults appeared to decline from March 1992 to April 1993.

Rhipicephalus pravus group

The presence on a single impala of the larvae of a *Rhipicephalus pravus*-like tick that parasitizes scrub hares in the north of the KNP (Horak *et al.* 1993) represents an accidental infestation. This tick has been described by Walker *et al.* (2000) as belonging to a *Rhipicephalus* sp. near *R. pravus*.

Rhipicephalus simus

The adults of *R. simus* prefer equids, suids, large carnivores and large ruminants as hosts, and the immature stages prefer murid rodents (Norval & Mason 1981; Braack *et al.* 1996; Walker *et al.* 2000). The collection of only one male tick each from two impalas in regions where adults are plentiful on Burchell's zebras, warthogs and large carnivores (Horak *et al.* 1984; 1988b; 2000b), supports the view that impalas are not suitable hosts. The 16 larvae collected from a single impala at Skukuza, where the majority of red veld rats, *Aethomys chrysophilus*, are infested with the immature stages of *R. simus* (Braack *et al.* 1996), also represent an accidental infestation.

Rhipicephalus zambeziensis

The preferred hosts of all stages of development of *R. zambeziensis* are domestic and wild ruminants (Norval *et al.* 1982; Walker *et al.* 2000). Numerous adults have also been collected from lions and leopards, *Panthera pardus* (Horak *et al.* 2000b). The intensities of infestations of *R. zambeziensis* larvae and nymphs on impalas in the Biyamiti region were similar to those on greater kudus (Horak *et al.* 1992), but the intensity of infestation of adults was higher on kudus, similar to the pattern for *R. appendiculatus*.

The marked seasonal changes ($P < 0.001$) in the prevalences and intensities of infestations of all stages of *R. zambeziensis* were similar to those for *R. appendiculatus*. At Skukuza and in the Biyamiti region during 1980/81, *R. zambeziensis* larvae were present from March to October with a peak from April to August, nymphs were present from May to December with a July to October peak, and adults were present in all months except July 1980, with a

February to March peak (Fig. 4). With minor differences, the seasonal patterns were similar in all locations, and were similar to those on greater kudus in the Biyamiti region (Horak *et al.* 1992)

During 1980/81, the intensities of infestations of all three stages of *R. zambeziensis* were significantly higher at Skukuza than in the Biyamiti region ($P <$ 0.007) and at Crocodile Bridge ($P < 0.05$). The intensity of infestation of larvae was also significantly higher at Skukuza and Biyamiti than at Pafuri in July 1980 ($P = 0.003$), but no nymphs or adults were collected at Pafuri at this time. The intensities of infestations of all three stages were significantly higher at Skukuza than at Pafuri in 1992/93 ($P =$ 0.001), particularly during the peak periods.

In South Africa *R. zambeziensis* occurs in north-eastern Mpumalanga Province, in Limpopo Province and in the north-western regions of North West Province (Walker *et al.* 2000), and its distribution overlaps that of *R. appendiculatus* in the KNP. It is the more common species at Skukuza, whereas *R. appendiculatus* is more common at Crocodile Bridge and Pafuri. In Zimbabwe *R. zambeziensis* occurs in the lower, drier regions with mean annual rainfall of 400–700 mm, and *R. appendiculatus* is found in the higher, wetter regions with 500–2 000 mm mean annual rainfall. There is an overlap of the two species in the regions with 500–700 mm rainfall (Norval *et al.* 1982). The locations where impalas were collected in the KNP receive an average of 500–700 mm of rainfall, but the ratios of *R. zambeziensis* to *R. appendiculatus* were not consistent with the rainfall between locations. Not only was *R. appendiculatus* more common at Crocodile Bridge, which receives more rainfall than Skukuza, but also at Pafuri which receives less (Gertenbach 1980). Thus other factors such as local microclimatic conditions and habitats may influence the apparent abundance of the two species.

At Skukuza the prevalences of *R. zambeziensis* larvae and nymphs did not differ significantly between 1980/81 and 1992/93 ($P \geq 0.4$), but the intensities of infestations of both stages were significantly higher ($P \leq 0.001$) in 1980/81 than in 1992/93. There was a significant month x year interaction for both stages ($P \leq 0.035$) caused by the lower peak intensities of infestation in 1992/93. There was no difference in the prevalence or intensity of infestation of adults between years ($P \geq$ 0.54), but there was a significant month x year interaction ($P < 0.001$) as the intensity of infestation was higher from March to May 1992 than from March to May 1980, and higher from January to March 1981 than from January to March 1993. The lower intensities of infestations of *R. zambeziensis* larvae and nymphs in 1992/93 and the lower intensity of infestation of adults in 1993 probably reflect the influence of the 1992 drought on the free-living stages. However, the relative decrease was much less than the decrease in the numbers of *R. appendiculatus*, which exhibited marked decreases in the prevalences and intensities of infestation of all developmental stages. This is consistent with the greater sensitivity of *R. appendiculatus* to dry conditions.

The age/sex distribution of *R. zambeziensis* was similar to that of *R. appendiculatus*. In 1980/81 the prevalences and intensities of infestations of *R. zambeziensis* larvae and nymphs did not differ among the age classes ($P = 0.79$). The prevalence of adults did not differ among the age classes ($P =$ 0.55), but the intensities of infestations were higher on yearlings and adults than on lambs ($P < 0.001$), particularly during the peak periods. The prevalence of the three life stages of *R. zambeziensis* did not differ on adult male and female impalas ($P =$ 0.26), but the intensity of infestation of larvae was higher on adult female impalas than on adult males ($P = 0.005$), particularly during March and April 1981. The intensity of infestation of adults was higher on adult male impalas ($P = 0.029$), particularly during April and May. Combining the burdens of adult *R. zambeziensis* and *R. appendiculatus*, adult male impalas were more heavily infested than adult females ($P = 0.01$), with the largest differences from March to May. The prevalence and intensity of infestation of adult *R. zambeziensis* and *R. appendiculatus* combined was similar at Skukuza, Biyamiti and Crocodile Bridge ($P = 0.45$).

The intensities of infestations of *R. zambeziensis* larvae and adults were significantly higher ($P <$ 0.001 and $P = 0.03$ respectively) on the "terminal" impalas at Skukuza in the 1982 drought than on the apparently healthy impalas killed at the same time or on the impalas examined in 1980. The intensity of infestation of nymphs did not differ between the three groups. When the burdens of adult *R. appendiculatus* and *R. zambeziensis* were combined, the prevalence was higher ($P = 0.004$) on the impalas examined in 1980 (93 %) and on the "terminal" impalas in 1982 (90 %) than on the apparently healthy animals in 1982 (43 %). However, the intensity of infestation of the adult ticks was higher on the "terminal" impalas in 1982 than on those examined in 1980 or on the apparently healthy impalas killed in 1982 ($P = 0.01$).

LICE

Total louse burdens

The impalas were infested with five louse species, one of which, a *Linognathus* sp., has not been described. The four described species are regularly collected from impalas (Ledger 1973; 1980; Horak 1982; Horak *et al.* 1983c; Matthee *et al.* 1998). The dominant species differed among areas in the KNP, with *Damalinia elongata* the most numerous at Skukuza, *Linognathus aepycerus* the most numerous at Pafuri, *D. elongata* and *L. aepycerus* the primary species at Crocodile Bridge, and *L. aepycerus* and *Linognathus nevilli* the most common species in the Biyamiti region (Table 2).

The highest total louse burdens were recorded in the late winter/early spring (August to October) ($P =$ 0.026–0.17) and the lowest burdens in the summer (December to February) (Fig. 7). The seasonal patterns were the result of seasonal changes in the intensities of infestations of *Damalinia aepycerus* and *Linognathus aepycerus* (see below), and the decline in the summer is possibly related to the higher temperatures during this period. The seasonal pattern conforms to that observed in other studies of lice infesting impalas and other antelopes (Horak *et al.* 1983b; Horak, Sheppey, Knight & Beuthin 1986b; Matthee *et al.* 1998).

The total lice burdens were significantly higher at Skukuza than in the Biyamiti region ($P = 0.001$) in 1980/81. On adult males, the prevalence of lice at Skukuza (100 %) was significantly higher ($P = 0.031$) than in the Biyamiti region (77 %) and at Crocodile Bridge (58 %), and the total louse burden was higher at Skukuza than in the Biyamiti region and at Crocodile Bridge ($P = 0.06$). The total louse burdens were significantly higher at Skukuza during 1980/81 than during 1992/93 ($P < 0.001$) (Table 11), but did not differ significantly between Skukuza and Pafuri during the latter period ($P = 0.46$).

Lice tend to be parasites of young animals (Horak *et al.* 1983b; 1986b), and the total burdens were significantly higher on lambs and yearlings than on adult impalas ($P = 0.002$). Most louse species were present on lambs within a month of birth suggesting that they were passed from the dam. The burdens on adult impalas were higher on females than on males, but the differences were not statistically significant ($P = 0.17$).

The "terminal" impalas in 1982 had significantly higher total louse burdens than the apparently healthy impalas and those killed in 1980 ($P = 0.03$) (Table 11). The "terminal" impalas were obviously stressed and this probably lowered their resistance to lice, allowing effective and rapid translation from one developmental stage to the next. In addition, they probably lacked the energy to groom properly or conserved energy by reducing their grooming rate, thus allowing sustained levels of infestation.

Damalinia aepycerus

Damalinia aepycerus was collected at all locations in the KNP, and although it was the most numerous species on impalas in the Nylsvley Nature Reserve, Limpopo Province (Horak 1982), it was never so in the KNP. The preferred biotopes of *D. aepycerus* are the body and tail, with 60.4 % of the population present in the former and 36.0 % in the latter site (Matthee *et al.* 1998).

The intensity of infestation of *D. aepycerus* was significantly higher at Skukuza than in the Biyamiti region and at Crocodile Bridge in 1980/81 ($P < 0.03$). At Skukuza, the intensity of infestation did not differ significantly between 1980/81 and 1992/93 ($P >$ 0.17), nor did the intensity of infestation differ significantly between Skukuza and Pafuri during 1992/93 ($P = 0.34$). In 1980/81 there were two apparent peaks in the intensity of infestation (Fig. 7), one in April or March caused by high infestations on lambs and yearlings, and a more generalized peak in the late winter/spring (August to October). However, in 1992/93 the peak infestations occurred from March to May 1992 and the intensity of infestation declined through 1993. There was no clear seasonal pattern in the intensity of infestation on impalas in the Nylsvley Nature Reserve (Horak 1982), while Matthee *et al.* (1998) reported the highest intensities of infestation in February and July on impala ewes examined on Letaba Ranch, Limpopo Province during February, July and October.

The intensity of infestation of *D. aepycerus* was higher on lambs and yearlings than on adult impalas ($P = 0.065$). Infestation of lambs occurred within a month after birth. The prevalence and intensity of infestation on adult impalas did not differ significantly between sexes ($P = 0.12$). The prevalence and intensity of infestation did not differ among the three groups of impalas at Skukuza compared for the effects of the 1982 drought ($P =$ 0.18 and 0.81 respectively). The prevalence of adult lice was higher on the "terminal" and apparently healthy impalas in the 1982 drought (100 % and 90 % respectively) than on those examined in

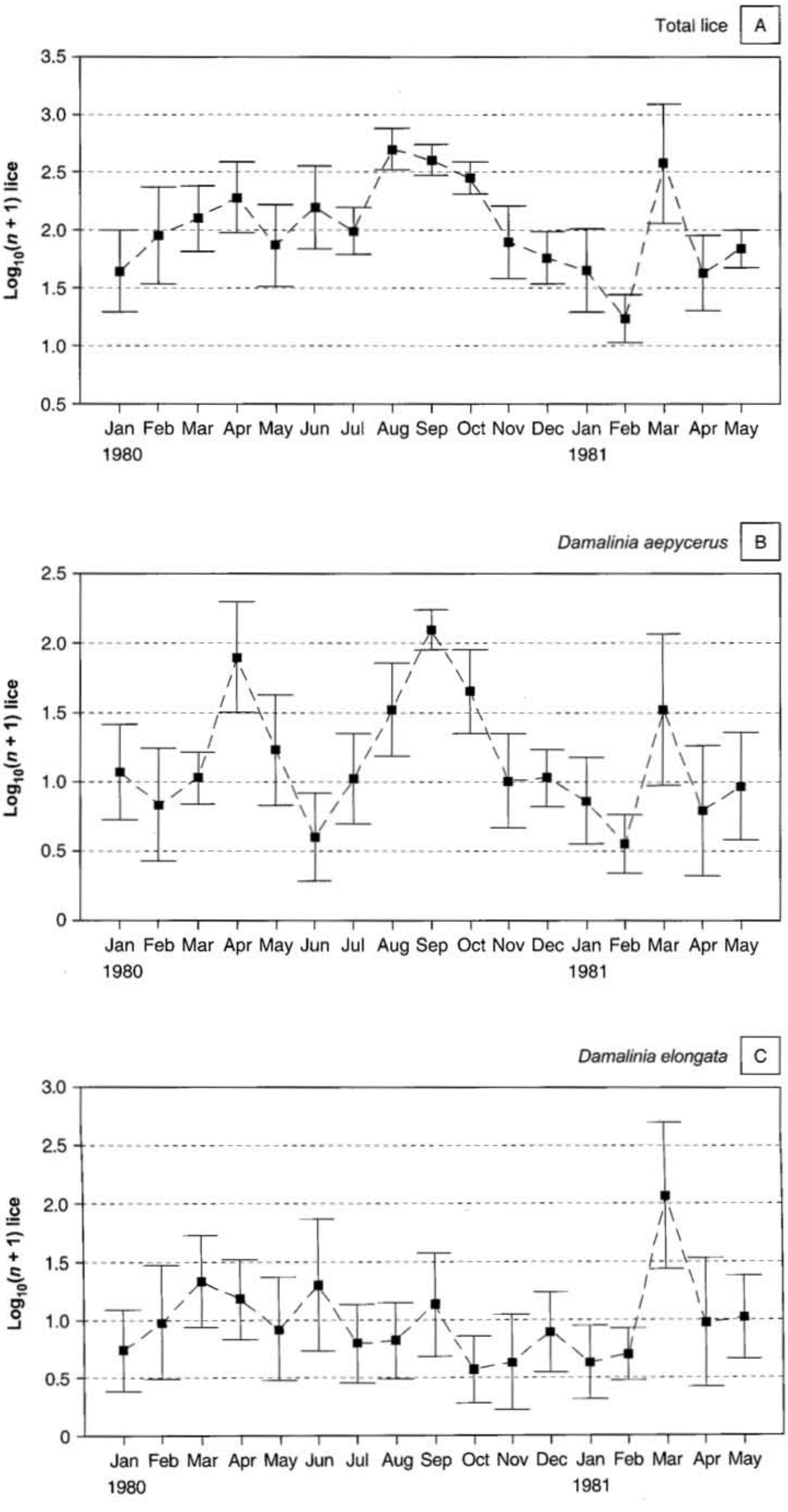

FIG. 7

Seasonal pattern of the intensity of infestation of [A] the total lice burden (x ± 1SE), [B] *Damalinia aepyceus* (x ± 1SE), and [C] *Damalinia elongata* (x ± 1SE) on impalas at Skukuza and in the Biyamiti region during 1980/81. No lambs were collected after January 1981 and no yearlings after February 1981. The monthly sample at each locality ranged from two to six or seven impalas

1980 (57 %), but the intensity of infestation did not differ among the three groups ($P = 0.13$).

Damalinia elongata

Damalinia elongata was the most numerous louse species on impalas at Skukuza in 1980/81 and 1992/93, and accounted for much of the higher louse burden at this locality in 1980/81. The prevalence and intensity of infestation were significantly higher ($P > 0.014$) at Skukuza than in the Biyamiti region in 1980/81. Although the intensity of infestation was higher on adult male impalas at Skukuza than at Crocodile Bridge, the difference was not statistically significant ($P > 0.1$). The prevalence of *D. elongata* at Skukuza did not differ significantly between 1980/81 and 1992/93 ($P > 0.25$), but the intensity of infestation was significantly higher in 1980/81 than in 1992/93 ($P = 0.004$). The intensity of infestation was similar at Skukuza and Pafuri in July 1980, but only two adult *D. elongata* were collected at Pafuri in 1992/93.

There was no seasonal pattern in the prevalence or intensity of infestation of *D. elongata* (Fig. 7). Lambs were infested by 2 months of age. The intensity of infestation was higher on yearlings than on adult impalas ($P = 0.044$), with the most pronounced differences at Skukuza. The prevalence and intensity of infestation on adult impalas did not differ significantly between sexes ($P > 0.31$). At Skukuza, the prevalence and intensity of infestation did not differ among the three groups of animals compared to assess the effect of the 1982 drought ($P = 0.46$). The intensity of infestation appears to be much higher on the "terminal" impalas, but one individual accounted for > 91 % of the total burden, and only four of ten "terminal" animals were infested.

Linognathus aepycerus

Even though the greatest numbers of *L. aepycerus* were collected from the body, this louse appears to be spread fairly evenly over the whole skin surface if the much larger surface area of the body, as opposed to those of the head, neck, legs and tail is taken into account (Matthee *et al.* 1998). It was the most common louse at Pafuri, and was also common in the Biyamiti region and at Crocodile Bridge. The prevalence of *L. aepycerus* on adult male impalas did not differ between Skukuza, the Biyamiti region and Crocodile Bridge in 1980/81 ($P > 0.3$), but the intensity of infestation was marginally higher at Skukuza than in the Biyamiti region ($P = 0.078$). At Skukuza the prevalence of *L. aepycerus* did not differ significantly between 1980/81 and 1992/93 ($P > 0.58$), but the intensity of infestation was higher in 1980/81 than in 1992/93 ($P = 0.02$). The prevalence of infestation (100 % and 87.5 % respectively) did not differ significantly ($P = 0.12$) between Pafuri and Skukuza in 1992/93, but its intensity was significantly higher at Pafuri than at Skukuza ($P < 0.02$).

There was a strong seasonal pattern in both the prevalence and intensity of infestation ($P < 0.02$) of *L. aepycerus* at Skukuza and in the Biyamiti region during 1980/81, with the highest prevalence and intensity of infestation from July to October (Fig. 8). The intensity of infestation was similar in the two areas from July to October, but tended to be higher at Skukuza in the other months. The seasonal pattern was similar at Skukuza in 1980/81 and 1992/93, but there was a significant month x location interaction between Skukuza and Pafuri in 1992/93. The intensity of infestation at Pafuri declined from March 1992 to February 1993, with only a slight increase in October 1992, whereas the pattern at Skukuza was similar to that in Fig. 11. Matthee *et al.* (1998) recorded the highest intensity of infestation with *L. aepycerus* during October on Letaba Ranch, but there was no clear seasonal pattern on impalas in the Nylsvley Nature Reserve (Horak 1982).

Lambs were infested with *L. aepycerus* within the first month after birth, and the prevalence and intensity of infestation were significantly higher on lambs than on adult impalas ($P \leq 0.004$). The prevalence and intensity of infestation on adult animals did not differ significantly between the sexes ($P > 0.16$). The prevalence and intensity of infestation of *L. aepycerus* were higher on impalas in the 1982 drought than on the animals examined in 1980 ($P \leq 0.04$), but did not differ ($P > 0.1$) between the "terminal" and the apparently healthy animals in 1982.

Linognathus nevilli

Linognathus nevilli was originally collected and described from around the feet of impalas (Ledger 1973), and is most commonly found on the feet and hind legs (Matthee *et al.* 1998). Small numbers may also be present on the head, neck and body, possibly transferred there when these regions are scratch-groomed with the hind feet, an action illustrated by Mooring (1995).

The prevalence and intensity of infestation of *L. nevilli* did not differ between Skukuza, the Biyamiti region and Crocodile Bridge in 1980/81 ($P > 0.3$). At Skukuza, the prevalence was marginally higher

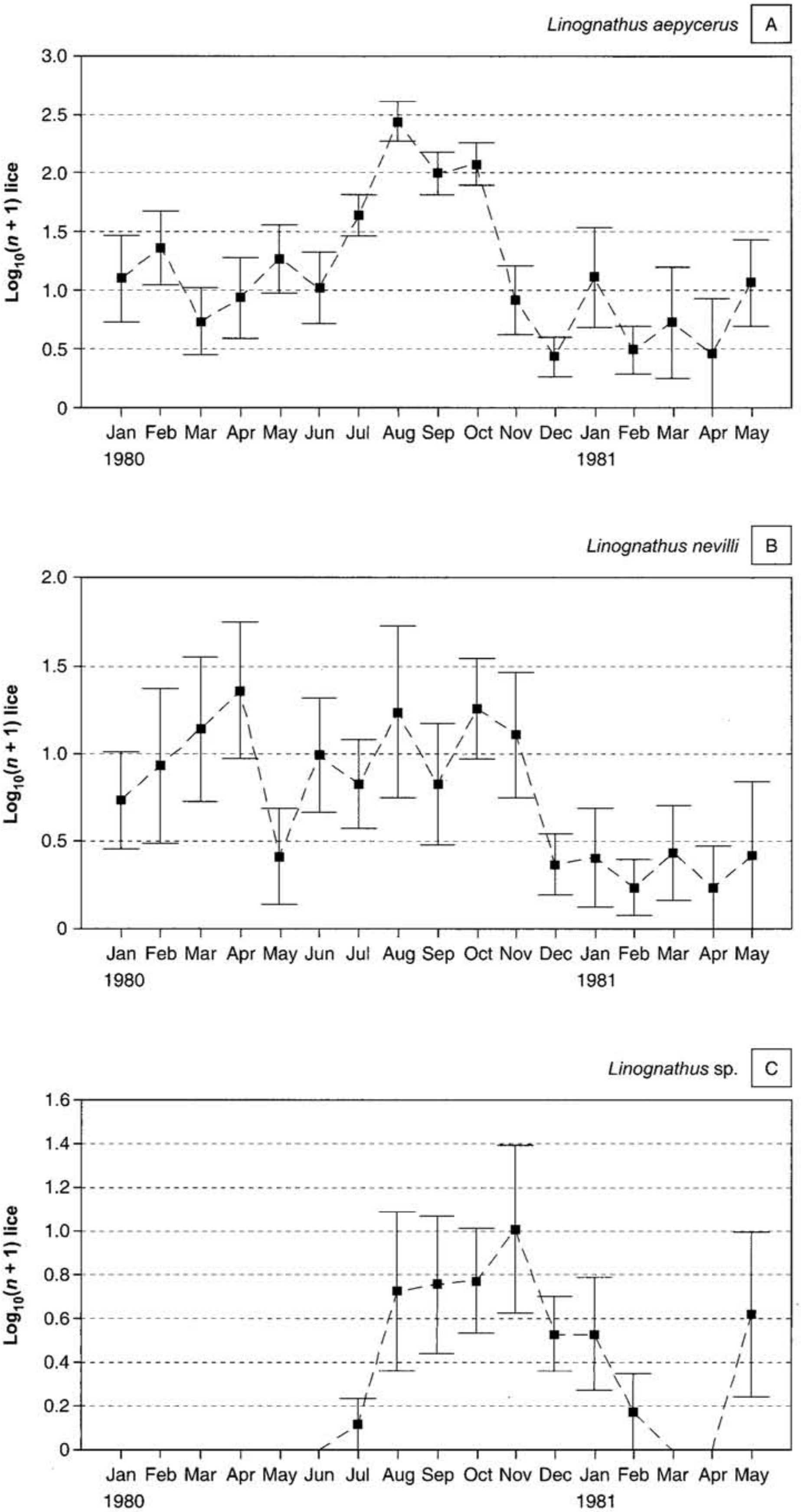

FIG. 8

Seasonal pattern of the intensity of infestation of [A] *Linognathus aepycerus* (x ± 1SE), [B] *Linognathus nevilli* (x ± 1SE), and [C] *Linognathus* sp. (x ± 1SE) on impalas at Skukuza and in the Biyamiti region during 1980/81. No lambs were collected after January 1981 and no yearlings after February 1981. The monthly sample at each locality ranged from two to six or seven impalas

($P = 0.09$) and the mean intensity of infestation was significantly higher ($P < 0.001$) in 1980/81 than in 1992/93. The prevalence did not differ significantly between Pafuri and Skukuza ($P = 0.15$), but the intensity of infestation was significantly higher at Pafuri ($P = 0.023$).

Although there were two apparent peaks, one in the late summer and early autumn, and another in the late winter and spring, there was no clear seasonal pattern in the intensity of infestation of *L. nevilli* at Skukuza and in the Biyamiti region during 1980/81 (Fig. 8). The seasonal patterns at Skukuza were statistically significant ($P = 0.008$) in the comparison of 1980/81 and 1992/93, and were more pronounced in 1980/81. No seasonal pattern was evident in the comparison of Skukuza and Pafuri in 1992/93 ($P = 0.41$). The prevalence of *L. nevilli* was significantly higher ($P < 0.001$) on lambs (81 %) and yearlings (68 %) than on adult impalas (37 %), and the intensity of infestation was significantly higher on lambs than on yearlings ($P < 0.05$), and higher on yearlings than on adult impalas ($P < 0.01$). No *L. nevilli* were collected from lambs until they were a month old. The prevalence and intensity of infestation of *L. nevilli* were significantly higher on adult female impalas than on adult males ($P \leq 0.006$).

Although the prevalence and intensity of infestation of nymphs were higher on the "terminal" impalas than on the apparently healthy animals in 1982 ($P = 0.05$ and 0.09, respectively), the prevalence and intensity of infestation of *L. nevilli* did not differ significantly between the three groups of animals ($P = 0.21$).

Linognathus sp.

Although this louse accounted for only a small percentage of the lice collected, it was common, with an overall prevalence of 27.4 %. The prevalence and intensity of infestation did not differ between Skukuza and the Biyamiti region in 1980/81, or between Skukuza and Pafuri in 1992/93 ($P = 0.35$). At Skukuza the prevalence did not differ between 1980/81 and 1992/93 ($P = 0.74$) but the intensity of infestation was higher in 1980/81 than in 1992/93 ($P = 0.01$). The prevalence was considerably lower ($P = 0.004$) on adult male impalas (9 %) than on adult females (39 %), and none were collected from the adult males at Crocodile Bridge.

The intensity of infestation of *Linognathus* sp. peaked in late winter to early summer (Fig. 8). None were collected at Skukuza or in the Biyamiti region from January to June 1980, but they were present during some of these months in 1981 and 1992/93. The1992/93 peak at Skukuza occurred in September and was of shorter duration than the peak in 1980/81. The prevalence of *Linognathus* sp. did not differ among age classes ($P = 0.44$), but the intensity of infestation was higher on lambs than on yearlings and adults ($P = 0.01$). Infestation of the lambs took place within the first month after birth. The prevalence and intensity of infestation did not differ among the "terminal" and apparently healthy impalas examined during the 1982 drought and those examined in 1980 ($P = 0.49$).

FLIES

The impalas were infested with the hippoboscid flies *Hippobosca fulva* and *Lipoptena paradoxa*.

Hippobosca fulva

According to Haeselbarth *et al.* (1966) the main hosts of *H. fulva* are probably small antelopes such as steenbok, *Raphicerus campestris*, common duikers, *Sylvicapra grimmia*, and Kirk's dik-diks, *Madoqua kirkii*, with impalas also being infested. However, we have not collected this fly from steenbok or common duikers in South Africa (I.G.H. unpublished observations 1999), and although they were collected from impalas in Swaziland, none were collected from common duikers (Gallivan & Surgeoner 1995).

The *H. fulva* collected in the current surveys do not represent the actual numbers infesting impalas in the KNP. Large numbers of these flies are visible on the white underside and perineum of impalas, where they are frequently mistaken for ticks. However, when the impalas were shot, many of them took flight and only those still present in the haircoat were collected when the carcasses were processed for tick recovery.

The prevalence and intensity of infestation of *H. fulva* were significantly higher ($P = 0.003$) on impalas in the Biyamiti region than at Skukuza during 1980/81. On adult males the prevalence was higher ($P = 0.05$) in the Biyamiti region (62 %) than at Skukuza (29 %) and Crocodile Bridge (17 %), but the intensity of infestation did not differ significantly among the three locations ($P = 0.10$). The prevalence and intensity of infestation of *H. fulva* were significantly lower (P 0.001) in spring and mid-summer than in autumn and winter (Fig. 9) on the impalas at Skukuza and in the Biyamiti region during 1980/81. The seasonal pattern in the intensity

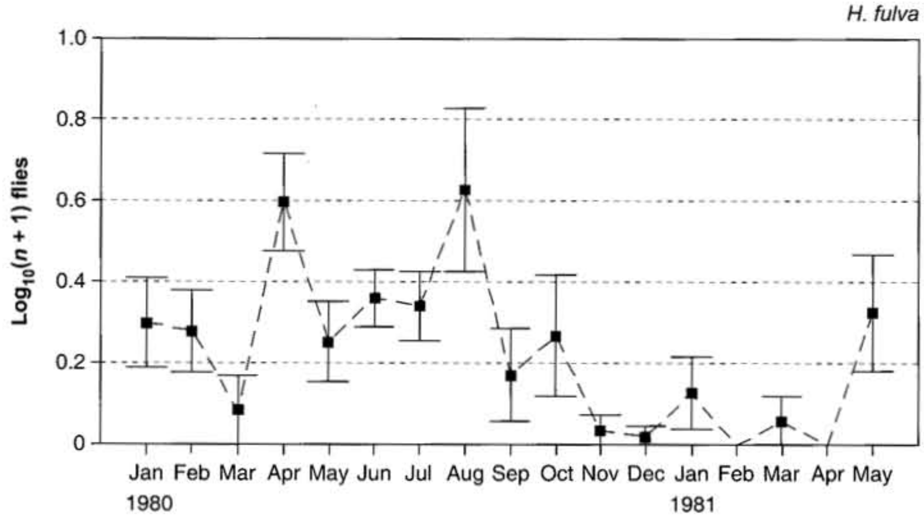

FIG. 9 Seasonal pattern of the intensity of infestation of *Hippobosca fulva* (x ± 1SE) on impalas at Skukuza and in the Biyamiti region during 1980/81. No lambs were collected after January 1981 and no yearlings after February 1981. The monthly sample at each locality ranged from two to six or seven impalas

of infestation of *H. fulva* on impalas at these localities during 1980/81 was almost the exact opposite to that noted for *L. paradoxa* on greater kudus in the Biyamiti region (Visagie, Horak & Boomker 1992). These different seasonal patterns could reflect differences in the months during which the majority of flies of the two species emerge from pupae, or differences in seasonal habitat usage by the two host species.

The prevalence and intensity of infestation of *H. fulva* did not differ among age classes ($P > 0.43$), or between the sexes of adult impalas ($P > 0.26$). Prevalence did not differ among the groups of impalas examined during the drought of 1982 and the group examined during 1980 at Skukuza ($P = 0.44$), it was, however, low during the months in which these animals were examined.

Lipoptena paradoxa

Lipoptena paradoxa is common on nyalas, bushbuck and greater kudus, and is also frequently encountered on common duikers (Visagie *et al.* 1992). All these antelopes utilize woodland habitats (Skinner & Smithers 1990). Once the fly has found a host its wings break off and it becomes a permanent parasite. Only five impalas examined during 1980/81 were infested with *L. paradoxa*, one in the Biyamiti region and four at Skukuza, and no flies were collected from adult male animals at Crocodile Bridge. Its presence on impalas must be regarded as coincidental as they frequently share woodland habitats with greater kudus.

General discussion

This paper summarises the results of several collections of arthropod parasites of impalas made over a 13-year period in the KNP. Despite differences in the age and sex composition of the animals in the surveys, we were able to examine the effects of location, season, age, sex, and two droughts. The seasonal patterns for each species of tick and louse are discussed above. The remaining factors are summarized below.

There were several differences in the ixodid tick species among locations. *Boophilus decoloratus* was most common in the Biyamiti region, while *A. hebraeum* larvae and nymphs were most common at Skukuza and Crocodile Bridge, *A. marmoreum* larvae at Skukuza, *R. evertsi evertsi* in the Biyamiti region and at Pafuri, and *R. zambeziensis* at Skukuza. *Rhipicephalus appendiculatus* larvae and nymphs were more common in the Biyamiti region and at Crocodile Bridge and Pafuri than at Skukuza, but *R. appendiculatus* adults were most common at Skukuza. [Several of the adult ticks collected from impalas at Skukuza, and identified as *R. appendiculatus*, could actually have been *R. zambeziensis* because of the difficulty of distinguishing between these species in the adult stage (Walker *et al.* 2000)]. Rainfall and temperature are important factors determining the distribution and abundance of tick species. However, the apparent abundance of tick species was not consistent with the rainfall and temperature patterns within the KNP. Part of this inconsistency may be caused by differential habitat use within heterogenous landscape types where differences in microclimates create marked differences in tick challenge (Minshull & Norval 1982). The presence of preferred or alternate hosts may also be a factor. The higher intensity of infestation of *R. appendiculatus* adults at Skukuza differs from the patterns in the intensities of infestation of the larvae and nymphs. This may, however, be due to the difficulty experienced in specifically identifying the adults as discussed above. Impalas appear to be good hosts for the immature stages of *R. appendiculatus* but poor hosts for the adults. However, in Swaziland where impalas were the most numerous ungulate species and there were few large ungulates, they were important hosts of *R. appendiculatus* adults (Gallivan & Surgeoner 1995).

The intensities of infestation of the lice *D. aepycerus* and *D. elongata* were higher at Skukuza than in the Biyamiti region and at Crocodile Bridge, while *L. aepycerus* and *L. nevilli* were more common at Pafuri. These differences in the louse populations are not easily explained, but may be due to climatic differences, or differences in the age composition of the impala populations. At Pafuri impalas tend to become older than elsewhere in the KNP because of a lower density of lions, and very old animals in this region are often unable to groom effectively because their dental grooming apparatus has become worn down (McKenzie 1990).

It is often assumed that young animals are the most prone to infestation, but the total tick burdens, and the burdens of *B. decoloratus* and *B. decoloratus* adults, *A. hebraeum* nymphs and adults, *R. appendiculatus* nymphs and adults, *R. zambeziensis* nymphs and adults, and *R. evertsi evertsi* adults were higher on yearling and adult impalas than on lambs. In contrast, with the exception of *D. elongata*, the intensity of infestation of lice was higher on lambs. The lower burdens of *B. decoloratus* on lambs were caused by a low intensity of infestation on newborn lambs in December, and the low intensity of infestation of larvae indicates that these lambs had not yet been exposed. With the exception of *B. decoloratus*, the differences among age classes were similar to those reported for tick prevalence on impalas in Swaziland (Gallivan *et al.* 1995). The lower intensities of infestations of the nymph and adult stages of ixodid ticks on impala lambs may be a function of the higher allogrooming rate of these animals (Mooring & Hart 1992). This would presumably be effective in removing the larger nymphal and adult ticks, but less so in removing the larvae. The age distribution of lice infestation conforms to observations on other species that lice tend to be parasites of young animals and that infestation occurs early in life (Horak *et al.* 1983b; 1986b; Horak, MacIvor & Greeff 2001).

The prevalence of adult *A. hebraeum* and the intensities of infestations of adult *R. appendiculatus* and *R. zambeziensis* were higher on adult male impalas than on adult females, while the intensities of infestations of *R. zambeziensis* and *R. appendiculatus* larvae were higher on adult female impalas. The higher prevalence of adult *A. hebraeum* and intensity of infestation of adult *R. appendiculatus* on adult male impalas are similar to the pattern in Swaziland (Gallivan *et al.* 1995). Gallivan *et al.* (1995) reported an increased prevalence of *B. decoloratus* adults on male impalas, and Mooring & Hart (1995) reported increased infestations of *B. decoloratus* and *R. zambeziensis* on adult male impalas during the rut in the Omay Communal lands in Zimbabwe. The differences reported for *B. decoloratus* may be caused by variations in sampling techniques among the three studies.

The contrasts in the intensities of infestations of adult *R. appendiculatus* and *R. zambeziensis* between the sexes were most pronounced during the rut. Mooring & Hart (1995) suggest that the increase in testosterone during the rut reduces immunity in the males. However, this should cause an increase in the intensity of infestation of all stages of ticks. The intensities of infestations of *R. appendiculatus* and *R. zambeziensis* larvae were actually higher on the adult female than on the adult male impalas during the rut. The higher intensities of infestations of adult *R. appendiculatus* and *R. zambeziensis* on adult male impalas during the rut are most likely caused by a reduction in grooming activity (Mooring & Hart 1995). The higher intensities of infestations of *R. appendiculatus* and *R. zambeziensis* larvae on the adult female impalas may be the consequence of increased exposure. Adult male impalas have restricted home ranges during the rut, whereas the home range of the females encompasses several male territories (Murray 1982). Because peak activity of *R. appendiculatus* and *R. zambeziensis* larvae occurs during the rut, the mobile female impalas are more likely to be exposed to them.

In contrast to the ticks, lice tended to be more common on adult female impalas than on adult males, and the differences were statistically significant for *L. nevilli* and *Linognathus* sp. Female impalas occur in larger herds, maintain shorter distances between neighbours and allogroom more frequently than males (Mooring 1995), all factors that could facilitate the transfer of lice between individuals. Both *L. nevilli* and *Linognathus* sp. have relatively low prevalences and intensities of infestation, and increased interaction among females may be essential to maintain transmission.

The collections included two droughts, in 1982 and in 1992 (Fig. 1). The 1982 collections were made in November and early December, following an extended period of low rainfall beginning in February 1982, and the 1992/93 collections began at the end of the summer after a year of low rainfall and continued through a year of normal rainfall. Consequently the collections represent different phases of the drought. The 1982 collections were also preceded by two years of above normal rainfall and impala populations, while the 1992/93 collections were preceded by two years of below average rainfall and impala populations.

In 1982 there was an increase in the total tick and louse burdens on the "terminal" impalas, primarily because of the increase in the intensities of infestations of *B. decoloratus* and *L. aepycerus*, and the burden of *D. elongata* on one individual. There was also an increase in the intensities of infestations of adult *A. hebraeum*, *R. appendiculatus*, *R. evertsi evertsi* and *R. zambeziensis*. These patterns reflect the seasonal activity of the ticks and lice, and are consistent with a reduction in resistance in animals in poor condition. There were few differences in the tick and louse burdens between the "apparently healthy" impalas in 1982 and those examined in 1980. In 1992/93 there was a reduction in the intensities of infestations of all tick and louse species relative to 1980/81. The reductions in the louse burdens and intensities of infestations of *R. zambeziensis* larvae and nymphs were proportional to the reduction in the size of the impala population, indicating that the availability of the hosts was a major factor in maintaining ectoparasite populations. The reductions in the infestations of *A. hebraeum*, *B. decoloratus*, *R. evertsi evertsi* and *R. appendiculatus* in 1992/93 relative to 1980/81 were greater than the reduction in the impala population. The drier environmental conditions probably reduced the survival of the free-living stages of these species as there was a greater reduction in the number of questing *B. decoloratus* larvae than *R. zambeziensis* larvae (Spickett *et al.* 1995), and *R. zambeziensis* tolerates drier conditions than *R. appendiculatus*. Thus, while the collections in the 1982 drought indicate that the immediate impact of a drought may be an increase in ectoparasite infestations because of the nutritional stress, the collections in the 1992 drought suggest that a reduction in impala populations as well as reduced survival of the free-living ticks may reduce the ectoparasite burdens over time.

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REFERENCES

ACOCKS, J.P.H. 1988. *Veld types of South Africa*. Memoirs of the Botanical Survey of South Africa, No. 57.

BAKER, MAUREEN K. & DUCASSE, F.B.W. 1967. Tick infestation of livestock in Natal. I. The predilection sites and seasonal variations of cattle ticks. *Journal of the South African Veterinary Medical Association*, 38:447–453.

BAKER, MAUREEN K. & KEEP, M.E. 1970. Ckecklist of the ticks found on the larger game animals in the Natal game reserves. *Lammergeyer*, 12:41–47.

BEZUIDENHOUT, J.D. & STUTTERHEIM, C.J. 1980. A critical evaluation of the role played by the red-billed oxpecker *Buphagus erythrorhynchus* in the biological control of ticks. *Onderstepoort Journal of Veterinary Research*, 47:51–75.

BRAACK, L.E.O., HORAK, I.G., JORDAAN, LEONORA, SEGERMAN, JOYCE & LOUW, J.P. 1996. The comparative host status of red veld rats (*Aethomys chrysophilus*) and bushveld gerbils (*Tatera leucogaster*) for epifaunal arthropods in the Eastern Transvaal Lowveld. *Onderstepoort Journal of Veterinary Research,* 63:149–158.

CLARKE, FRANCOISE C., ELS, D.A., HELLER-HAUPT, A., RECHAV, Y. & VARMA, M.G.R. 1989. Expression of acquired immunity to immature stages of the tick *Rhipicephalus evertsi evertsi* by rabbits and guinea-pigs. *Medical and Veterinary Entomology*, 3:35–39.

COLBO, M.H. 1973. Ticks of Zambian wild animals: a preliminary checklist. *Puku*, no. 7:99–105.

COLBORNE, J.R.A. 1989. The role of wild hosts in maintaining tick populations on cattle in the southeastern lowveld of Zimbabwe. M. Phil. thesis, University of Zimbabwe.

DE CASTRO, J.J., NEWSOM, R.M. & HERBERT, L.V. 1989. Resistance in cattle against *Rhipicephalus appendiculatus* with an assessment of cross-resistance to *R. pulchellus* (Acari: Ixodidae). *Experimental and Applied Acarology*, 6: 237–244.

DOWER, KATHY M., PETNEY, T.N. & HORAK, I.G. 1988. The developmental success of *Amblyomma hebraeum* and *Amblyomma marmoreum* on the leopard tortoise, *Geochelone pardalis*. *Onderstepoort Journal of Veterinary Research*, 55:11–13.

GALLIVAN, G.J. & SURGEONER, G.A. 1995. Ixodid ticks and other ectoparasites of wild ungulates in Swaziland: regional, host and seasonal patterns. *South African Journal of Zoology*, 30:169–177.

GALLIVAN, G.J., CULVERWELL, J., GIRDWOOD, R. & SURGEONER, G.A. 1995. Ixodid ticks of impala (*Aepyceros melampus*) in Swaziland: effect of age class, sex, body condition and management. *South African Journal of Zoology*, 30:178–186.

GALLIVAN, G.J. & HORAK, I.G. 1997. Body size and habitat as determinants of tick infestations of wild ungulates in South Africa. *South African Journal of Wildlife Research*, 27:63–70.

GERTENBACH, W.P.D. 1980. Rainfall patterns in the Kruger National Park. *Koedoe*, 23:35–43.

GERTENBACH, W.P.D. 1983. Landscapes of the Kruger National Park. *Koedoe*, 26:9–121.

HAESELBARTH, E., SEGERMAN, J. & ZUMPT, F. 1966. *The arthropod parasites of vertebrates in Africa south of the Sahara (Ethiopian Region). III. (Insecta excl. Phthiraptera)*. [Johannesburg]: The South African Institute for Medical Research (Publication no. 52).

HART, B.L. & HART, LYNETTE A. 1992. Reciprocal allogrooming in impala, *Aepyceros melampus*. *Animal Behaviour*, 44: 1073–1083.

HORAK, I.G. 1982. Parasites of domestic and wild animals in South Africa. XV. The seasonal prevalence of ectoparasites on impala and cattle in the northern Transvaal. *Onderstepoort Journal of Veterinary Research*, 49:85–93.

HORAK, I.G., POTGIETER, F.T., WALKER, JANE B., DE VOS, V. & BOOMKER, J. 1983a. The ixodid tick burdens of various large ruminant species in South African nature reserves. *Onderstepoort Journal of Veterinary Research*, 51:221–228.

HORAK, I.G., DE VOS, V. & BROWN, MOIRA R. 1983b. Parasites of domestic and wild animals in South Africa. XVI. Helminth and arthropod parasites of blue and black wildebeest (*Connochaetes taurinus* and *Connochaetes gnou*). *Onderstepoort Journal of Veterinary Research*, 50:243–255.

HORAK, I.G., BOOMKER, J., KINGSLEY, SHIRLEY A. & DE VOS, V. 1983c. The efficacy of ivermectin against helminth and arthropod parasites of impala. *Journal of the South African Veterinary Association*, 54:251–253.

HORAK, I.G., DE VOS, V. & DE KLERK, B.D. 1984. Parasites of domestic and wild animals in South Africa. XVII. Arthropod parasites of Burchell's zebra, *Equus burchelli*, in the eastern Transvaal Lowveld. *Onderstepoort Journal of Veterinary Research*, 51:145–154.

HORAK, I.G., KNIGHT, M.M. & DE VOS, V. 1986a. Parasites of domestic and wild animals in South Africa. XX. Arthropod parasites of the Cape mountain zebra (*Equus zebra zebra*). *Onderstepoort Journal of Veterinary Research*, 53:127–132.

HORAK, I.G., SHEPPEY, K., KNIGHT, M.M. & BEUTHIN, C.L. 1986b. Parasites of domestic and wild animals in South Africa. XXI. Arthropod parasites of vaal ribbok, bontebok and scrub hares in the western Cape Province. *Onderstepoort Journal of Veterinary Research*, 53:187–197.

HORAK, I.G., MACIVOR, K.M. DE F., PETNEY, T.N. & DE VOS, V. 1987. Some avian and mammalian hosts of *Amblyomma hebraeum* and *Amblyomma marmoreum* (Acari: Ixodidae). *Onderstepoort Journal of Veterinary Research*, 54: 397–403.

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

HORAK, I.G., BOOMKER, J., DE VOS, V. & POTGIETER, F.T. 1988b. Parasites of domestic and wild animals in South Africa. XXIII. Helminth and arthropod parasites of warthogs, *Phacochoerus aethiopicus*, in the eastern Transvaal Lowveld. *Onderstepoort Journal of Veterinary Research*, 55: 145–52.

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

HORAK, I.G., SPICKETT, A.M., BRAACK, L.E.O. & WILLIAMS, E.J. 1991. Parasites of domestic and wild animals in South Africa. XXVII. Ticks on helmeted guineafowls in the eastern Cape Province and eastern Transvaal Lowveld. *Onderstepoort Journal of Veterinary Research*, 58:137–143.

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

HORAK, I.G., SPICKETT, A.M., BRAACK, L.E.O. & PENZHORN, B.L. 1993. Parasites of domestic and wild animals in South Africa. XXXII. Ixodid ticks on scrub hares in the Transvaal. *Onderstepoort Journal of Veterinary Research*, 60:163–174.

HORAK, I.G., SPICKETT, A.M., BRAACK, L.E.O., PENZHORN, B.L., BAGNALL, R.J. & UYS, A.C. 1995a. Parasites of domestic and wild animals in South Africa. XXXIII. Ixodid ticks on scrub hares in the north-eastern regions of Northern and Eastern Transvaal and of KwaZulu-Natal. *Onderstepoort Journal of Veterinary Research*, 62:123–131.

HORAK, I.G., DE VOS, V. & BRAACK, L.E.O. 1995b. Arthropod burdens of impalas in the Skukuza region during two droughts in the Kruger National Park. *Koedoe*, 38:65–71.

HORAK, I.G., FOURIE, L.J. & VAN ZYL, J.M. 1995c. Arthropod parasites of impalas in the Kruger National Park with particular reference to ticks. *South African Journal of Wildlife Research*, 25:123–126.

HORAK, I.G. 1998. The relationships between ticks, hosts and the environment in the Kruger National Park, South Africa, in *The Second International Conference on Tick-borne Pathogens at the Host-Vector Interface: a Global Perspective, August 28 – September 1, 1995, Kruger National Park, South Africa: proceedings and abstracts*, edited by L. Coons & Marjorie Rothschild, 2:413–426.

HORAK, I.G. & BOOMKER, J. 1998. Parasites of domestic and wild animals in South Africa. XXXV. Ixodid ticks and bot fly larvae in the Bontebok National Park. *Onderstepoort Journal of Veterinary Research*, 65:205–211.

HORAK, I.G., SPICKETT, A.M. & BRAACK, L.E.O. 2000a. Fluctuations in the abundance of *Boophilus decoloratus* and three *Rhipicephalus* species on vegetation during eleven consecutive years. In *Proceedings of the Third International Conference on Ticks and Tick-borne Pathogens: into the 21st Century*. Institute of Zoology, Slovak Academy of Sciences, Bratislava, Slovakia, edited by M. Kazimírová, M. Labuda & P.A. Nuttall: 247–251.

HORAK, I.G., BRAACK, L.E.O., FOURIE, L.J. & WALKER, JANE B. 2000b. Parasites of domestic and wild animals in South Africa. XXXVIII. Ixodid ticks collected from 23 wild carnivore species. *Onderstepoort Journal of Veterinary Research*, 67:239–250.

HORAK, I.G., MACIVOR, K.M. DE F. & GREEFF, C.J. 2001. Parasites of domestic and wild animals in South Africa. XXXIX. Helminth and arthropod parasites of Angora goats in the southern Karoo. *Onderstepoort Journal of Veterinary Research*, 68:27–35.

LEDGER, J.A. 1973. A new species of *Linognathus* (Phthiraptera: Linognathidae) from the feet of an African antelope. *Journal of the Entomological Society of Southern Africa*, 36: 125–129.

LEDGER, J.A. 1980. *The arthropod parasites of vertebrates in Africa south of the Sahara. IV. Phthiraptera (Insecta).* [Johannesburg]: The South African Institute for Medical Research (Publication no. 56).

MACLEOD, J. 1970. Tick infestation patterns in the southern province of Zambia. *Bulletin of Entomological Research*, 60: 253–274.

MACLEOD, J. & MWANAUMO, B. 1978. Ecological studies of ticks (Acari: Ixodidae) in Zambia. IV. Some anomalous infestation patterns in the northern and eastern regions. *Bulletin of Entomological Research*, 68:409–429.

MASON, C.A. & NORVAL, R.A.I. 1980. The ticks of Zimbabwe. I. The genus *Boophilus*. *Zimbabwe Veterinary Journal*, 11: 36–43.

MATTHEE, SONJA, MELTZER, D.G.A. & HORAK, I.G. 1997. Sites of attachment and density assessment of ixodid ticks (Acari: Ixodidae) on impala (*Aepyceros melampus*). *Experimental and Applied Acarology*, 21:179–192.

MATTHEE, SONJA, HORAK, I.G. & MELTZER, D.G.A. 1998. The distribution and seasonal changes of louse populations on impala *Aepyceros melampus*. *South African Journal of Wildlife Research*, 28:22–25.

MCKENZIE, A.A. 1990. The ruminant dental grooming apparatus. *Zoological Journal of the Linnean Society*, 99:117–128.

MEESER, M.J.N. 1952. A preliminary survey of the endo- and ectoparasites of the impala - *Aepyceros melampus*. *Journal of the South African Veterinary Medical Association*, 23: 221–223.

MINSHULL, JACQUELINE I. & NORVAL, R.A.I. 1982. Factors influencing the spatial distribution of *Rhipicephalus appendiculatus* in Kyle Recreational Park, Zimbabwe. *South African Journal of Wildlife Research*, 12:118–123.

MOORING, M.S. & HART, B.L. 1992. Reciprocal allogrooming in dam-reared and hand-reared impala fawns. *Ethology*, 90: 37–51.

MOORING, M.S. 1995. The effect of tick challenge on grooming rate by impala. *Animal Behaviour*, 50:377–392.

MOORING, M.S. & MAZHOWU, W. 1995. Geographic distribution of ticks and comparison of tick load on male and female impala from three sites in Zimbabwe. *Zimbabwe Veterinary Journal*, 26:76–85.

MOORING, M.S. & HART, B.L. 1995. Differential grooming rate and tick load of territorial male and female impala, *Aepyceros melampus*. *Behavioural Ecology*, 6:94–101.

MOORING, M.S. & MCKENZIE, A.A. 1995. The efficiency of patch sampling for determination of relative tick burdens in comparison with total tick counts. *Experimental and Applied Acarology*, 19:533–547.

MURRAY, M.G. 1982. The rut of impala: aspects of seasonal mating under tropical conditions. *Zeitschrift fur Tierpsychologie*, 59:319–337.

NORVAL, R.A.I. 1975. Studies on the ecology of *Amblyomma marmoreum* Koch 1844 (Acarina: Ixodidae). *Journal of Parasitology*, 61:737–742.

NORVAL, R.A.I. & MASON, C.A. 1981. The ticks of Zimbabwe. II. The life cycle, distribution and hosts of *Rhipicephalus simus*, Koch 1844. *Zimbabwe Veterinary Journal*, 12:2–9.

NORVAL, R.A.I. 1981. The ticks of Zimbabwe. III. *Rhipicephalus evertsi evertsi*. *Zimbabwe Veterinary Journal*, 12:31–35.

NORVAL, R.A.I., WALKER, J.B. & COLBORNE, J. 1982. The ecology of *Rhipicephalus zambeziensis* and *Rhipicephalus appendiculatus* with particular reference to Zimbabwe. *Onderstepoort Journal of Veterinary Research*, 49:181–190.

NORVAL, R.A.I. 1983. The ticks of Zimbabwe. VII. The genus *Amblyomma*. *Zimbabwe Veterinary Journal*, 14:3–18.

PAINE, G.D. 1982. Ticks (Acari: Ixodoidea) in Botswana. *Bulletin of Entomological Research*, 72:1–16.

PETNEY, T.N., VAN ARK, H. & SPICKETT, A.M. 1990. On sampling tick populations: the problem of overdispersion. *Onderstepoort Journal of Veterinary Research*, 57:123–127.

RECHAV, Y., KNIGHT, M.M. & NORVAL, R.A.I. 1977. Life cycle of the tick *Rhipicephalus evertsi evertsi* Neumann (Acarina: Ixodidae) under laboratory conditions. *Journal of Parasitology*, 63:575–579.

RECHAV, Y., DAUTH, J., VARMA, M.G.R., CLARKE, F.C., ELS, D.A., HELLER-HAUPT, A. & DREYER, M.J. 1989. Changes in the concentration of globulins in naive guinea pigs during feeding by the immature stages of *Rhipicephalus evertsi evertsi* (Acari: Ixodidae). *Journal of Medical Entomology*, 26:247–251.

ROBERTSON, WENDY D. 1981. A four year study of the seasonal fluctuations in the occurrence of the blue tick *Boophilus decoloratus* (Koch) in the Coastal regions of the Eastern Cape, in *Proceedings of an International Conference on Tick Biology and Control*, Grahamstown, 27–29 January, 1981.

SANTOS DIAS, J.A.T. 1993. Some data concerning the ticks (Acarina-Ixodoidea) presently known in Mozambique. *Garcia de Orta, Serie Zoologie*, 18:27–48.

SHORT, N.J., FLOYD, R.B., NORVAL, R.A.I. & SUTHERST, R.W. 1989. Survival and behaviour of unfed stages of the ticks *Rhipicephalus appendiculatus*, *Boophilus decoloratus* and *B. microplus* under field conditions in Zimbabwe. *Experimental and Applied Acarology*, 6:215–236.

SKINNER, J.D. & SMITHERS, R.H.N. 1990. *Mammals of the southern African subregion*. Pretoria: University of Pretoria.

SPICKETT, A.M. & HEYNE, HELOISE 1990. The prehatch period and larval survival of *Boophilus decoloratus* (Koch, 1844) (Acarina: Ixodidae) under natural conditions in the Transvaal, South Africa. *Onderstepoort Journal of Veterinary Research*, 57:95–98.

SPICKETT, A.M., HORAK, I.G., VAN NIEKERK, ANDREA & BRAACK, L.E.O. 1992. The effect of veld-burning on the seasonal abundance of free-living ixodid ticks as determined by drag-sampling. *Onderstepoort Journal of Veterinary Research*, 59:285–292.

SPICKETT, A.M., HORAK, I.G., HEYNE, HELOIS & BRAACK, L.E.O. 1995. The effect of severe drought on the abundance of ticks on the vegetation and on scrub hares in the Kruger National Park. *Koedoe*, 38:59–63.

STUTTERHEIM, C.J. 1981. The feeding behaviour of the red-billed oxpecker. *South African Journal of Zoology*, 16:267–269.

THEILER, GERTRUD 1962. The Ixodoidea parasites of vertebrates in Africa south of the Sahara (Ethiopian region). Project S 9958. Report to the Director of Veterinary Services, Onderstepoort. 260 pp. Mimeographed.

VAN DYK, P.J. & MCKENZIE, A.A. 1992. An evaluation of the effectivity of the scrub technique in quantitative ectoparasite ecology. *Experimental and Applied Acarology*, 15:271–283.

VISAGIE, ELIZE J., HORAK, I.G. & BOOMKER, J. 1992. The louse fly *Lipoptena paradoxa* Newstead, 1907 (Diptera: Hippoboscidae): description of its adult and puparium and biology in South Africa. *Onderstepoort Journal of Veterinary Research,* 59:303–314.

WALKER, JANE B. 1974. *The ixodid ticks of Kenya. A review of present knowledge of their hosts and distribution.* London: Commonwealth Institute of Entomology.

WALKER, JANE B. 1991. A review of the ixodid ticks (Acari: Ixodidae) occurring in South Africa. *Onderstepoort Journal of Veterinary Research,* 58:81–105.

WALKER, JANE B., KEIRANS, J.E. & HORAK, I.G. 2000. *The genus* Rhipicephalus *(Acari, Ixodidae): a guide to the brown ticks of the world.* Cambridge: Cambridge University Press.

WHYTE, I.C. & JOUBERT, S.C.J. 1988. Blue wildebeest population trends in the Kruger National Park and the effects of fencing. *South African Journal of Wildlife Research,* 18:78–87.

YEOMAN, G.H. & WALKER, JANE B. 1967. *The ixodid ticks of Tanzania. A study of the zoogeography of the Ixodidae of an east African country.* London: Commonwealth Institute of Entomology.

ZIEGER, U., HORAK, I.G., CAULDWELL, A.E., UYS, A.C. & BOTHMA, J.DU P. 1998. The effect of chemical tick control on cattle on free-living ixodid ticks and on ticks parasitic on sympatric impala in the Central Province, Zambia. *South African Journal of Wildlife Research,* 28:10–15.