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Ixodid ticks and other ectoparasites of wild ungulates in Swaziland: regional, host and seasonal patterns

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Ixodid ticks and other ectoparasites were collected from impala (*Aepyceros melampus*), blue wildebeest (*Connochaetes taurinus*), kudu (*Tragelaphus strepsiceros*), common duiker (*Sylvicapra grimmia*) and warthog (*Phacochoerus aethiopicus*) in the Mlawula-Mbuluzi-Simunye Nature Reserve and Protected Area complex and Hlane Wildlife Sanctuary in the Swaziland lowveld, and from blue wildebeest and warthog in Malolotja Nature Reserve in the highveld from October 1985 to August 1986. The most commonly collected ticks were *Amblyosomma hebraeum, Boophilus decoloratus, Rhipicephalus appendiculatus, R. evertsi evertsi, R. maculatus, R. muehlensi* and *R. simus*. The diversity and intensity of infestation were greater in the lowveld, where the ectoparasite community was similar to that reported from these host species in the eastern Transvaal lowveld and Kwazulu/Natal. *A. hebraeum* was collected throughout the year, but the largest samples were in October and November when the animals were in poor condition. The seasonal occurrence of *R. appendiculatus* adults on impala was later than that reported for other host species, possibly owing to seasonal changes in habitat use. Seasonal changes in habitat use and temperature effects on pre-oviposition and development of the eggs may have caused the seasonal patterns in the occurrence of *B. decoloratus*.

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Introduction

Swaziland is a small country in south-eastern Africa bordered by Mozambique on the east, and surrounded on the north, west and south by the eastern Transvaal and Kwazulu/Natal in South Africa (Figure 1). Despite its small size, Swaziland is ecologically diverse with four main physiographic regions characterized by differences in elevation, soil type, temperature, rainfall and vegetation (Murdoch 1970; Goudie & Price-Williams 1983). Several studies of the ectoparasites of ungulates in the eastern Transvaal and Kwazulu/Natal have been published, but the only published surveys from Swaziland are those of Theiler (1948) and Wedderburn, Jagger, McCartan & Hunter (1991). These were confined to the ixodid ticks of cattle and other domestic animals. In the present paper we report on the ixodid ticks and other ectoparasites of some of the wild ungulates. The host-parasite associations, differences between regions, and the seasonal patterns of the more common ixodid ticks are described.

Materials and Methods

Study areas

This study was conducted in the Mlawula-Mbuluzi-Simunye Nature Reserve and Protected Area complex (Mlawula complex) and Hlane Wildlife Sanctuary in the north-eastern Swaziland lowveld, and in Malolotja Nature Reserve in the highveld along the western border (Figure 1).

The Mlawula complex covers an area of approximately 23000 ha. The mean annual rainfall over a 35-year period (1952–1986) was approximately 700 mm (Tambankulu Estates, unpubl. obs.). Most of the rain falls in the hot summers, and the winters are cool and dry (Figure 2). The mean daily relative humidity exceeds 75% during the summer and declines to 65% in the late winter (K. Braun, pers. comm.). The ungulates were collected in the western part of the complex (altitude: ± 200 m). Most of this area is over the basalt of

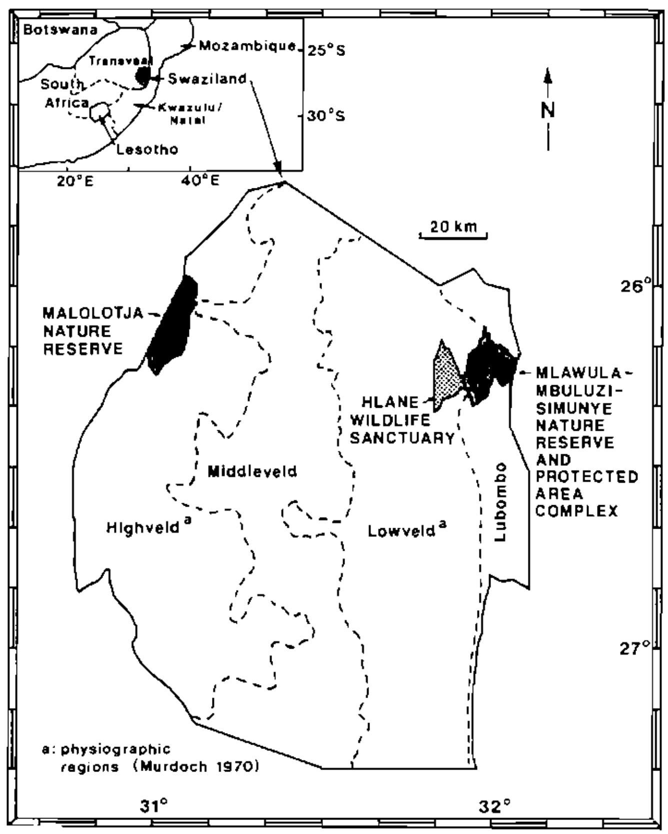

Figure 1 Map of Swaziland showing the locations of the Nature Reserves where the samples were collected.

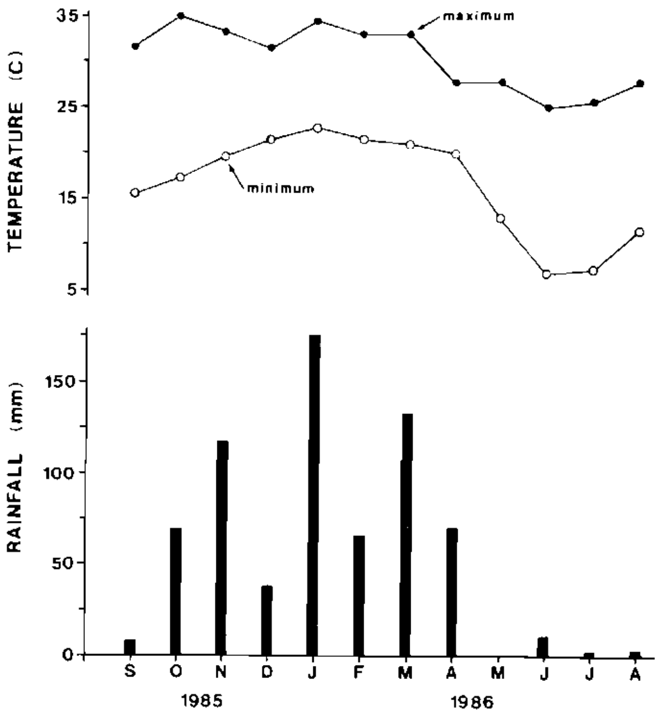

Figure 2 Monthly rainfall and mean maximum and minimum temperatures in the Mlawula-Mbuluzi-Simunye Nature Reserve and Protected Area complex from September 1985 to August 1986.

the eastern Swaziland lowveld (Murdoch 1970), but there are several rhyolite ridges associated with the Lubombo, a large rhyolite intrusion along the border between Mozambique and Swaziland and South Africa. The vegetation on the basalt is predominately *Acacia nigrescens, Sclerocarya birrea, Themeda triandra* savanna (lowveld, type 10; Acocks 1975), with a mixed *Combretum* spp. woodland on the rhyolite ridges.

Hlane Wildlife Sanctuary covers an area of 14200 ha adjacent to the south-western border of the Mlawula complex. The collections were made towards the western part of the sanctuary in an area of *Spirostachys africana, Euclea divinorum* bushveld overlying the grey shales of the Ecca series (Gertenbach & Potgieter 1978). Mean annual rainfall is less than 635 mm (Goudie & Price-Williams 1983).

Malolotja Nature Reserve covers an area of approximately 18000 ha along the western border of Swaziland. All of the ungulates were collected in the middle third of the reserve (altitude: ± 1200 m). This area overlies a complex geology dominated by quartzite conglomerate (Murdoch 1970). The annual rainfall is approximately 1250 mm. The seasonal patterns in rainfall and temperature are similar to those in the Mlawula-Mbuluzi-Simunye complex, but the temperatures are 5–10°C cooler (Goudie & Price-Williams 1983; K. Braun, pers. comm.). The central portion of Malolotja is a *T. triandra, Loudetia simplex* grassland (north-eastern mountain sourveld, type 8; Acocks 1975) with several old fields dominated by *Cynodon dactylon*.

Ungulate collection

The ungulate populations in the Mlawula complex and Malolotja Nature Reserve at the time of this study are listed in Table 1. Ectoparasites were collected from impala (*Aepyceros melampus*), blue wildebeest (*Connochaetes taurinus*), kudu (*Tragelaphus strepsiceros*), common (grey) duiker (*Sylvicapra grimmia*) and warthog (*Phacochoerus aethiopicus*) which were shot between October 1985 and August 1986, either during the culling programmes in the reserves or for research purposes. Impala were collected monthly, with sample sizes of 7–24 animals per month. The other species were collected at 1–3-month intervals when the opportunity arose. Sample sizes ranged from 1–5 animals per collection. All five species were collected in the Mlawula complex, but only blue wildebeest and warthog were collected from Hlane Wildlife Sanctuary and Malolotja Nature Reserve.

Table 1 Populations of the major ungulate species in Mlawula-Mbuluzi-Simunye Nature Reserve and Protected Area Complex in the Swaziland lowveld and Malolotja Nature Reserve in the highveld. The species composition in Hlane Wildlife Sanctuary was similar to that in the Mlawula complex, but no recent population estimates were available

Reserve	Ungulate species	Population
Mlawula-Mbuluzi-Simunye Nature Reserve and Protected Area Complex[1]	Impala (*Aepyceros melampus*)	4000+
	Blue wildebeest (*Connochaetes taurinus*)	100
	Kudu (*Tragelaphus strepsiceros*)	400
	Nyala (*Tragelaphus angasii*)	40
	Waterbuck (*Kobus ellipsiprymnus*)	60
	Warthog (*Phacochoerus aethiopicus*)	200
	Zebra (*Equus burchelli*)	150
	White rhinoceros (*Ceratotherium simum*)	12
Malolotja Nature Reserve (Central Area)[2]	Blue wildebeest (*Connochaetes (taurinus*)	390
	Blesbok (*Damaliscus dorcas phillipsi*)	171
	Warthog (*Phacochoerus aethiopicus*)	34
	Zebra (*Equus burchelli*)	58

[1] — estimated populations in 1986 (K. Braun, pers. comm.). Other species present included: common duiker (*Sylvicapra grimmia*), common reedbuck (*Redunca arundinum*), mountain reedbuck (*Redunca fulvorofula*), bushbuck (*Tragelaphus scriptus*) and steenbok (*Rhapicerus campestris*).

[2] — from game count in November 1985 (T. Ballance, pers. comm.). Other species present included: impala (*Aepyceros melampus*), common duiker (*Sylvicapra grimmia*), mountain reedbuck (*Redunca fulvorofula*), vaal rhebok (*Pelea capreolus*) and oribi (*Ourebia ourebi*).

Ectoparasite collection

Samples of ectoparasites were collected in 70% ethanol when the ungulates were necropsied. In October and November 1985 the presence or absence, and relative load (light, moderate or heavy), of visible ectoparasites on each impala was noted, but samples were only collected from some individuals. Ectoparasites were collected from all of the impala from December 1985 to August 1986, and from all of the other ungulates. All of the visible ectoparasites were collected from four warthog and from other animals with a low level of infestation, but only samples were collected when the infestations were large. Each collection was made over a 10–15-min

Table 2 Prevalence (%) of ixodid ticks and other ectoparasites on wild ungulates in the Mlawula-Mbuluzi-Simunye Nature Reserve and Protected Area complex and Hlane Wildlife Sanctuary in the Swaziland lowveld

Ectoparasite	Stage	Host: Impala (155)[1]	Blue Wildebeest (4)	Kudu (6)	Common Duiker (5)	Warthog (19)
Ixodid ticks						
Amblyomma hebraeum	adult	12,9	100,0	66,7	20,0	78,9
(Koch, 1844)		(0,5)[2]	(19,0)	(6,5)	S	(61,4)[3]
	nymph	35,5	25,0	33,3	40,0	94,7
	larva	8,4	0	0	0	15,8
Boophilus decoloratus	adult	60,0	75,0	83,3	0	0
(Koch, 1844)		(2,6)	(4,8)	(3,5)		
	nymph	27,7	25,0	16,7	0	0
	larva	29,0	25,0	16,7	0	0
Haemaphysalis leachi	adult	0,6	0	0	0	0
(Audouin, 1827)		S				
Hyalomma truncatum	adult	0	25,0	0	0	0
(Koch, 1844)			S			
Rhipicephalus appendiculatus	adult	61,9	25,0	66,7	60,0	47,4
(Neumann, 1901)		(8,2)	(9,0)	(64,0)	(0,6)	(5,3)
	nymph	32,3	0	33,3	40,0	26,3
	larva	23,3	0	0	20,0	15,8
Rhipicephalus evertsi evertsi	adult	49,0	100,0	83,3	20,0	0
(Neumann, 1897)		(1,3)	(11,3)	(8,2)	S	
	nymph	29,7	0	0	0	0
	larva	26,5	0	16,7	0	0
Rhipicephalus maculatus	adult	0	25,0	16,7	0	52,6
(Neumann, 1901)			S	S		(4,7)
	nymph	0	0	16,7	0	0
	larva	0	0	16,7	0	0
Rhipicephalus muehlensi	adult	93,6	0	100,0	0	10,5
(Zumpt, 1943)		(15,3)		(64,5)		(0, 1)
	nymph	46,5	0	33,3	20,0	5,3
	larva	32,3	0	16,7	0	0
Rhipicephalus reichenowi/zumpti	adult	0	0	0	0	5,2
						S
Rhipicephalus simus	adult	0,6	0	16,6	0	89,5
(Koch, 1844)		S		S		(7,0)[3]
Rhipicephalus sp.	adult	0	0	0	0	5,3
						S
Argasid ticks						
Ornithodoros porcinus porcinus	adult	0	0	0	0	10,5
(Walton, 1962)						(0,1)
Fleas						
Ctenocephalides felis		0	0	0	20,0	0
(Bouché, 1835)					S	
Echidnophaga larina		0	0	0	0	78,9
(Jordan & Rothschild, 1906)						(6,4)
Lice						
Linognathus sp.		P				
Linognathus aepyceros		P				
(Bedford, 1936)						
Hippoboscid flies						
Hippobosca fulva		8,4	0	0	0	0
(Austen, 1911)						
Lipoptena paradoxa		0	0	83,3	60,0	0
(Newstead, 1907)						

[1] — number of hosts examined. Impala samples are from December 1985 to August 1986; [2] — mean sample size of adults; [3] — includes warthog with complete counts; S — single specimen; P — present.

period by two observers, one of whom was the first author. The whole body was examined, with particular attention to the head, especially the ears, the legs, the axillary region, the belly, the groin and the peri-anal region. Excluding the four warthog with complete collections, the mean sample size of ticks (i.e. number collected per host), was 48.3, with a range of 0–474.

Collections of visible ectoparasites lead to an under-reporting of the true intensity of infestation, particularly of the immature stages and smaller adult ticks (MacIvor, Horak, Holton & Petney 1987). However, as the time for collections was restricted, and the hides were usually not available, neither complete collections of large numbers of visible ectoparasites nor destructive sampling procedures were deemed practical. Nevertheless, the samples do provide a minimum estimate of tick prevalence, and an index of the temporal changes in intensity of infestation of tick species. The searching time per tick was reduced at higher intensities of infestation, therefore it was easier to collect larger samples.

Results

The ixodid ticks and other ectoparasites of the ungulates from the lowveld and highveld are presented in Tables 2 and 3.

Ixodid ticks

The commonly collected ixodid ricks were *Amblyomma hebraeum, Boophilus decoloratus, Rhipicephalus appendiculatus R. evertsi evertsi, R. maculatus, R. muehlensi* and *R. simus.* The other species were limited to a single specimen each. There was a greater diversity of tick species in the lowveld, and a much higher intensity of infestation. Only *R. e. evertsi* and *R. simus* were collected in both areas. Based on the results of a Mann-Whitney *U* test (Zar 1974), the sample sizes of *R. simus* from warthog did not differ between the lowveld and highveld ($p > 0{,}2$), but the samples of *R. e. evertsi* from wildebeest were significantly larger in the lowveld than in the highveld ($p < 0.005$).

In the lowveld, duiker had the fewest species of ticks and the lowest intensity of infestation of adult ticks of any of the ungulates, and was the only host species from which more nymphs and larvae were collected than adult ticks. Kudu were often heavily infested with ticks, particularly *R. muehlensi* and *R. appendiculatus.*

A. hebraeum adults and nymphs were collected from all five species of ungulates. Adults were common on warthog, wildebeest and kudu, but the prevalence on impala and duiker was low, and the samples were usually small (≤ 3). Maturing females (Table 4) were collected from impala, warthog, wildebeest and kudu. Nymphs were collected more frequently than adults from impala, duiker and warthog. Adults, nymphs and larvae were collected throughout the year. There was no significant seasonal variation in the prevalence of adults on impala (Figure 3) or warthog ($p > 0{,}1$), but the largest samples from impala, kudu, warthog and wildebeest were collected in October and early November prior to the spring rains. Nymphs were collected more frequently from impala in December and January than in June and July ($p = 0{,}035$), but there was no seasonal pattern on warthog.

All stages of *B. decoloratus* were collected from impala, wildebeest and kudu, and all three stages were collected in all months. *B. decoloratus* adults were common on impala in October and November, and the largest samples (24–28) were collected in October, December and January. The largest samples from kudu and wildebeest were collected in October. The prevalence of *B. decoloratus* adults on impala declined from December to June ($\chi^2_8 = 17{,}71$; $p = 0{,}024$), and the largest sample in July and August was six. Maturing *B. decoloratus* females were collected in all months.

R. appendiculatus adults were collected from all five species of ungulates, but maturing females were only collected from impala and kudu. Nymphs and larvae were collected from impala, duiker, kudu and warthog. Adults were only collected from February to August (Figure 3), and the seasonal change in prevalence on impala ($\chi^2_8 = 68{,}82$; $p \ll 0{,}001$) was paralleled by changes in the sample sizes. The largest samples

Table 3 Prevalence (%) of ixodid ticks and other ectoparasites of wild ungulates in Malolotja Nature Reserve in the Swaziland highveld

Ectoparasite	Stage	Host: Blue Wildebeest (18)[1]	Host: Warthog (3)
Ixodid ticks			
Ixodes sp.	adult	5,6 S	0
Rhipicephalus evertsi evertsi (Neumann, 1897)	adult	61,1 (2,4)[2]	0
Rhipicephalus follis (Dönitz, 1910)	adult	0	33,3 S
Rhipicephalus lunulatus (Neumann, 1907)	adult	5,6 S	0
Rhipicephalus simus (Koch, 1844)	adult	5,6 S	66,7 (1,7)
Fleas			
Echidnophaga larina (Jordan & Rothschild, 1906)		0	33,3

[1] — number of hosts examined; [2] — mean sample size in brackets; S — single specimen.

Table 4 Size criteria for engorging female ticks which should detach within 24 h (Horak, Boomker, De Vos & Potgieter 1988a; Horak, Fourie, Novellie & Williams 1991)

Species	Length (mm)
Amblyomma hebraeum	9,0
Boophilus decoloratus	4,0
Rhipicephalus appendiculatus	5,0
Rhipicephalus evertsi evertsi	6,0
Rhipicephalus maculatus[1]	6,0
Rhipicephalus muehlensi[1]	4,0
Rhipicephalus simus	6,0

[1] — the length is estimated from the relative length of the unengorged females

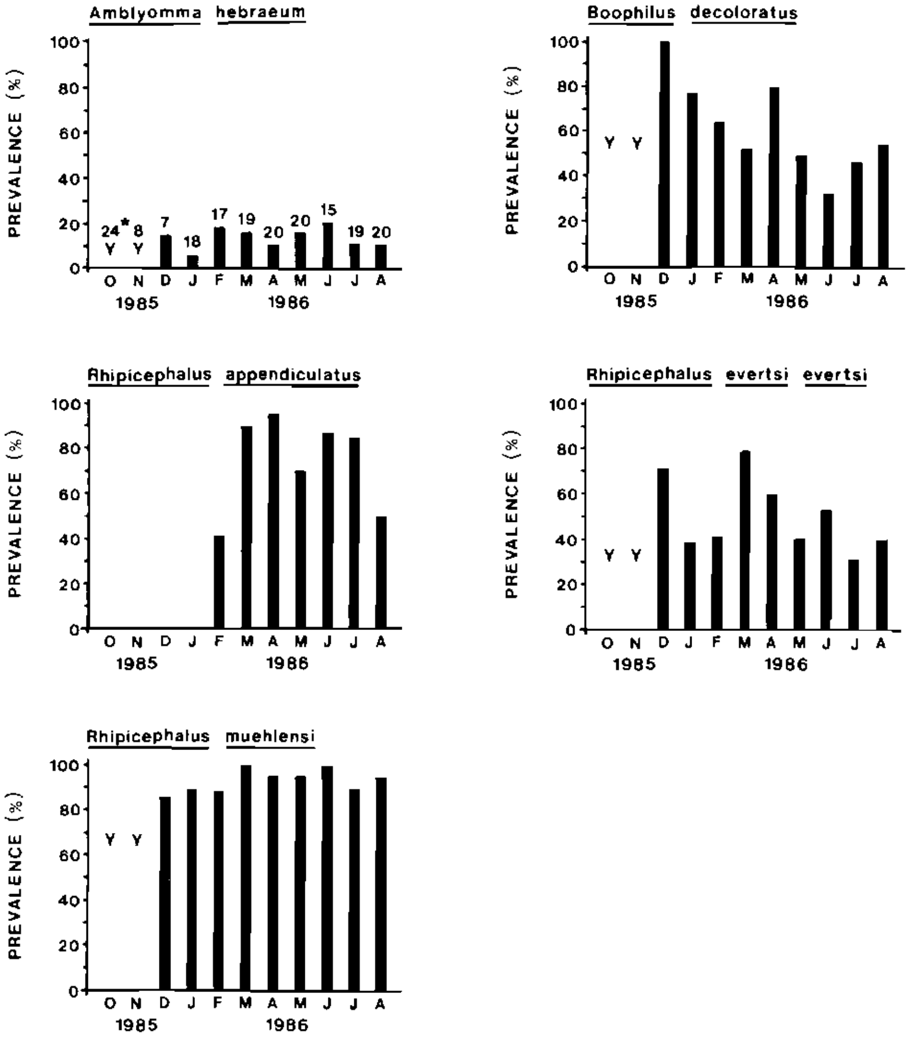

Figure 3 Monthly prevalence of adults of the five major tick species of impala. '*' is the number of impala collected that month. 'Y' indicates that the tick was collected, but the prevalence was not determined.

from individual impala were 13 in February, 95 in March, and only 5 in August. Maturing females were collected from 26% of the impala infested with adult *R. appendiculatus* from March to June (n = 62). Larvae were collected from April to August, and nymphs from October to December and May to August, with large samples from impala in July and August.

R. e. evertsi adults were found only on antelope, with maturing females on impala, wildebeest and kudu. Nymphs and larvae were collected from impala and kudu. All three stages were collected throughout the year. There was no significant seasonal trend in the prevalence (Figure 3) or sample sizes on impala.

R. maculatus adults were collected from November to May, with the largest samples in February. They were primarily ticks of warthog. Nymphs and larvae were collected from one kudu in May.

R. muehlensi adults, including maturing females, were common on impala and kudu. Nymphs were collected from impala, duiker, kudu and warthog, and larvae from impala and kudu. All three stages were collected throughout the year, and there were no significant differences in the seasonal prevalence of adults, maturing females, nymphs or larvae in the December to August collections from impala. The largest samples of adults were collected from January to June, and large samples of nymphs were collected in July and August.

R. simus was primarily a warthog tick, with only single specimens from the antelope. It was present throughout the year, but the largest samples were collected in the summer.

Other ectoparasites

The other ectoparasites were not as obvious as the ixodid ticks and were less likely to be collected. The flea, *Echidnophaga larina*, was collected from warthog in the lowveld and highveld, and the argasid tick, *Ornithodoros porcinus porcinus*, was collected from warthog in the lowveld. *Ctenocephalides felis* was collected from duiker. Two species of hippoboscid flies, *Lipoptena paradoxa* and *Hippobosca fulva*, were collected in the lowveld. *L. paradoxa* was collected from kudu and duiker, and *H. fulva* was collected from impala. The lice, *Linognathus aepyceros* and *Linognathus* sp., were incidental collections.

Discussion

Distribution

The ectoparasite community in the Swaziland lowveld was similar to that in the Kruger National Park and Kwazulu/Natal. The major differences in species composition between the Swaziland lowveld and Kruger National Park were the occurrence of *R. muehlensi* and the absence of *R. zambeziensis*. *R. muehlensi*, which has not been reported from Swaziland previously, is a tick of the eastern African coastal region (Walker 1991). In Swaziland it may be restricted to the eastern end of the Mbuluzi River watershed which contains several coastal plant and animal species (J. Culverwell, pers. comm.). *R. zambeziensis* is restricted to drier, hotter areas (Norval, Walker & Colborne 1982).

Other ixodid ticks which have not been reported previously from Swaziland were: *R. maculatus*, *R. follis*, *R. lunulatus* and *R. reichenowi/zumpti*. *R. maculatus*, *R. follis* and *R. lunulatus* have been reported from the eastern Transvaal and Kwazulu/Natal (Baker & Keep 1970; Walker, Keirans, Pegram & Clifford 1988; Walker 1991; Spickett, Horak, Van Niekerk & Braack 1992), and *R. follis* may be widespread in Swaziland (J.B. Walker, pers. comm.). Our specimen of *R. reichenowi/zumpti* was originally classified as *R. reichenowi* based on the description in Matthysse & Colbo (1987), but Dr Walker and Prof. Horak tentatively called it *R. zumpti*. There is, however, some confusion in the nomenclature of the *R. reichenowi/zumpti* species complex as *R. zumpti* was sunk as a synonym of *R. reichenowi* by Clifford and Anastos in 1962 (Walker 1966). *R. reichenowi* is widespread in Mozambique (Walker 1966), and *R. zumpti* has been reported from Kwazulu/Natal (Baker & Keep 1970; Horak, Boomker & Flamand 1991).

The distribution of *A. hebraeum*, *R. e. evertsi* and *H. truncatum* conformed to the distribution of these ticks within Swaziland reported by Theiler (1948, 1950, 1956). However, no *B. decoloratus* or *R. appendiculatus* were collected in Malolotja Nature Reserve even though these two species have been collected in the Swaziland highveld (Theiler 1949a; 1949b; Wedderburn *et al*. 1991).

The absence of *B. decoloratus* and *R. appendiculatus*, and the lower ectoparasite burdens, in Malolotja Nature Reserve may result from a number of factors. The original blue wildebeest and warthog populations had been translocated from the lowveld (T. Ballance, pers. comm.) where blue wildebeest were infested with *B. decoloratus* and *R. appendiculatus*, and warthog were infested with *R. appendiculatus*. However, blue wildebeest are not as efficient as hosts of *B. decoloratus* as other ungulates (Horak, De Vos & De Klerk 1984), and neither species appears to be a preferred host for *R. appendiculatus*. As blue wildebeest were the most abundant ungulate in the central portion of Malolotja Nature Reserve, and the host density was much lower than in the lowveld, the limited numbers of suitable hosts may have been one factor limiting tick populations.

A second factor limiting tick populations may have been the lower temperatures in Malolotja Nature Reserve. The average temperatures during the winter (May to August) at Mbabane and Piggs Peak in the Swaziland highveld, which are at a lower elevation and less exposed than the central region of Malolotja Nature Reserve, are 10 to 15°C (Goudie & Price-Williams 1983). At 15°C pre-oviposition and oviposition of *B. decoloratus* are prolonged, and egg output is reduced (Londt 1974; 1977). Eggs do not hatch below 15°C in the laboratory (Londt 1977) or 10°C in the field (Spickett & Heyne 1990). The eggs and immature stages of *R. appendiculatus* do not survive below 12°C (Tukahirwa 1976). The preference of wildebeest for the old fields and recent burns (T. Ballance, pers. comm.) may have accentuated the temperature effects. Short, open grasslands are subject to more extreme temperature fluctuations, and do not appear to be a suitable habitat for the larvae of many tick species (Londt & Whitehead 1972; Petney, Horak & Rechav 1987; Short, Floyd, Norval & Sutherst 1989). The preference of blue wildebeest for short, lawn-like grasslands (Smithers 1983) may provide an explanation for their apparent tick resistance.

Host-parasite associations

Most of the host-parasite associations have been reported previously. New host records were: *Haemaphysalis leachi* on impala, *R. follis* on warthog, and *R. lunulatus* on blue wildebeest. *H. leachi* is primarily a carnivore tick which occasionally infests ungulates (Matthysse & Colbo 1987), and *R. follis* and *R. lunulatus* have been collected from a range of ungulate hosts (Walker 1991). *Hippobosca fulva* was not collected from grey duiker which was listed as one of the primary hosts by Haeselbarth, Segerman & Zumpt (1966).

Warthog appeared to be the most important hosts for *A. hebraeum*, *R. maculatus* and *R. simus*. Although *A. hebraeum* adults were collected from the antelope, the intensity of infestation was never as large as on warthog. Nymphs were collected more frequently than adults from impala and duiker, supporting the suggestion that smaller ungulates serve as hosts for the immature stages while larger ungulates are more important hosts for the adults (Horak, MacIvor, Petney & De Vos 1987). However, the occurrence of maturing females on impala indicates that they can also serve as definitive hosts for the adult ticks.

The antelope were infested with *B. decoloratus*, *R. appendiculatus*, *R. e. evertsi* and *R. muehlensi*. *R. appendiculatus* was collected from all of the host species, with samples of adults from individual warthog and blue wildebeest greater than the total number of *R. appendiculatus* adults collected from 51 warthog and 47 blue wildebeest respectively in Kruger National Park (Horak, De Vos & Brown 1983; Horak, Boomker, De Vos & Potgieter 1988a). Nevertheless, impala and kudu were probably the most important hosts. It has been suggested that small antelope such as impala are inefficient hosts of *R. appendiculatus*, and that populations can only be maintained when there are large ungulates present (Yeoman & Walker 1967; Horak 1982). However, the large number of *R. appendiculatus* adults, including maturing females, indicates that impala are suitable hosts for the adults as well as the nymphs and larvae.

R. muehlensi appears to be primarily a bush tick. Impala and kudu were the most important hosts, and large numbers were collected from bushbuck (*Tragelaphus scriptus*) and nyala (*T. angasii*) in Kwazulu/Natal (Horak, Potgieter, Walker, De Vos & Boomker 1983; Horak, Keep, Flamand & Boomker 1988b). Kudu, bushbuck and nyala are browsers, while impala are intermediate feeders, browsing for much of the year (Smithers 1983). Grazers such as reedbuck (*Redunca arundinum*) and buffalo *Syncerus caffer* support fewer *R. muehlensi* (Horak *et al*. 1983; 1988b) and no *R. muehlensi* were collected from blue wildebeest in Swaziland or Kwazulu/Natal (Baker & Keep 1970), although one waterbuck (*Kobus ellipsiprymnus*) from Mbuluzi Nature Reserve was heavily infested (Gallivan, unpubl. obs.).

Seasonality

The lack of a seasonal pattern in the prevalence and intensity of infestation of *R. e. evertsi* conforms to published observations, as does the spring/summer peak in *B. decoloratus* and the summer peak in intensity of infestation of *R. simus*. The seasonal patterns for *A. hebraeum* and *R. appendiculatus* differed from those described previously.

There does not appear to be a seasonal pattern in the intensity of infestation of *A. hebraeum* on warthog and kudu in Kruger National Park (Horak *et al.* 1988a; Horak, Boomker, Spickett & De Vos 1992), and on cattle the intensity of infestation is highest in the summer after the spring rains (Petney, Horak & Rechav 1987). In the present study there was no seasonal pattern in prevalence in the December to August samples from impala, or on warthog. However, the largest samples from all of the host species were collected in October and November prior to the spring rains. The apparent seasonality in the present study may been due to the association between *A. hebraeum* and body condition (Gallivan, Culverwell, Girdwood & Surgeoner 1995). There was less than 10 mm rainfall from mid-May to mid-October, and many of the animals were in poor condition at the end of the dry season. *A. hebraeum* was more common on impala, warthog, kudu and wildebeest in poor condition (Gallivan *et al.* 1995), and Horak *et al.* (1988a) reported that warthog in Kruger National Park were more heavily infested with *A. hebraeum* in a drought year.

In southern Africa *R. appendiculatus* is distinctly seasonal, with one life cycle a year. The seasonal occurrence of larvae (March to August) and nymphs (April to December) was similar to that reported previously (Baker & Ducasse 1967; Horak 1982; Minshull & Norval 1982; Horak *et al.* 1992), but *R. appendiculatus* adults were not collected from impala until February and were still present in August. This is later than the activity period (November to March) reported for cattle (Baker & Ducasse 1967; Horak 1982) and for the peak activity on kudu (January to May) in Kruger National Park (Horak *et al.* 1992). No *R. appendiculatus* adults were collected from the other ungulates in November or December, but all were infested in late Febntary and May.

Short & Norval (1981) have proposed a model with four factors which limit adult *R. appendiculatus* activity: (i) an average monthly minimum temperature < 15°C, (ii) < 10 mm rainfall per month, (iii) < 11 h of daylight, and (iv) an average maximum temperature >30°C with < 20 mm rainfall per month. Factors (i) and (ii) were violated in the Mlawula complex from May to August (Figure 2), and there was < 11 h of daylight from mid-May to mid-August. Factor (iv) occurred in September 1985, but not in September 1986, and the long-term rainfall records suggest that it only occurred sporadically.

Minshull & Norval (1982) suggested that the spatial distribution of *R. appendiculatus* larvae, nymphs and adults was determined by the spatial distribution of the hosts in different seasons. Seasonal changes in habitat use may also affect the timing of the activity periods.

Kudu are browsers and impala are predominately browsers during the winter (Smithers 1983), and during the hot, dry season (September and October) impala spend part of the day in the shade (Jarman & Jarman 1973). Nymphal activity is highest in the winter and early spring. Thus, engorged nymphs will detach in treed areas which are cooler and have lower saturation deficits than grasslands (Londt & Whitehead 1972; Minshull & Norval 1982). The development period of *R. appendiculatus* nymphs increases at lower temperatures (Branagan 1973) and adults enter a four to six-week period of behavioural quiesence after the moult (Minshull & Norval 1982). However, adults developing from nymphs which detached in July or August should have been active by mid-November at the temperatures in the Mlawula complex (Figure 2).

Seasonal shifts in habitat use by kudu and impala have been reported in other studies (Simpson 1972; Mason 1976; Murray 1982; Skinner, Monro & Zimmerman 1984). In the Mlawula complex most of the ungulates were concentrated on the basalt near permanent water sources in the late winter and early spring, but impala and kudu dispersed onto the rhyolite ridges after the spring rains. Impala used *Acacia nilotica* thickets extensively in the winter, although males moved to these areas earlier when they established breeding territories. With the change in spatial distribution, impala and kudu would not be exposed to *R. appendiculatus* adults until later in the summer when they returned to areas used in the winter. Thus, infestation would be delayed.

The drop-off of nymphs in treed areas may also be a factor in the prolonged survival of adults. Minshull & Norval (1982) noted that *R. appendiculatus* adults, which are sensitive to temperature and humidity, were present in *Julbernardia* woodland for a longer period than in *Brachystegia* woodland or *Hyparrhenia* grassland, presumably because of more favourable microclimatic conditions. Nevertheless, prolonged survival may not guarantee reproduction as no maturing females were collected after June.

B. decoloratus was most common on impala in the late spring and summer and least common in the winter. The apparent seasonality of *B. decoloratus* may have been influenced by both the temperature sensitivity of development of the free-living stages and the seasonal shifts in habitat use. At the spring and summer temperatures in the Mlawula complex, pre-oviposition to larval hatch would take approximately six weeks (Londt 1974; 1977), whereas development of the free-living stages would take approximately four months in the winter. Eggs produced by females detaching in early March would hatch by May, but females detaching in April would not produce larvae until July or August. The delayed development in the winter produces a convergence of hatch in the spring, which will be accentuated by the increased survival of larvae at the cooler temperatures during the winter (Spickett & Heyne 1990). The spring hatch while the impala were concentrated on the basalt increased the probability that the larvae would find a host. The dispersal of impala after the spring rains would have allowed engorged female ticks to detach and infest the summer habitat, but larvae produced by female ticks detaching later in the summer would have had a lower probability of encountering a host when the impala shifted back to the basalt.

Little is known of the life history of *R. maculatus* and *R. muehlensi*. The largest samples of *R. maculatus* adults were collected from warthog in February and none were collected in July, suggesting a summer peak in adult activity. All three stages of *R. muehlensi* were collected throughout the year, and maturing females were collected from December to August. There was no significant seasonal variation in the prevalence of adults or nymphs on impala, but the largest samples of adults were collected in the summer and autumn and the largest samples of nymphs were collected in the spring.

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