The dynamics of questing ticks collected for 164 consecutive months off the vegetation of two landscape zones in the Kruger National Park (1988–2002). Part III. The less commonly collected species

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Despite many studies regarding tick ecology, limited information on long-term changes in tick populations exist. This study assessed the long-term population dynamics of the less frequently collected questing ixodid ticks in the Kruger National Park (KNP). From 1988 to 2002, monthly dragging of the vegetation was performed in three habitats (grassland, woodland and gully) at two sites in the KNP (Nhlowa Road, Landscape Zone 17, and Skukuza, Landscape Zone 4). *Amblyomma marmoreum* and *Rhipicephalus evertsi evertsi* were collected as larvae most commonly. Most *A. marmoreum* larvae were collected at Skukuza and numbers peaked from March to July. More *R. evertsi evertsi* larvae were collected at Nhlowa Road and numbers peaked in summer and in winter, while at Skukuza there was a single peak in spring. *Haemaphysalis elliptica*, *Rhipicephalus simus* and *Rhipicephalus turanicus* were collected as adults most commonly. More *Ha. elliptica* and *R. turanicus* were collected at Nhlowa Road than at Skukuza, while *R. simus* numbers from the two sites were approximately equal. *Ha. elliptica* were collected most often between February and June, and *R. simus* and *R. turanicus* during February and March. All three species were collected more frequently in gullies than in grassland or woodland. Their numbers increased in 1994/1995 following an eruption of rodents, the preferred hosts of the immature stages. The different host-seeking strategies of ticks largely determine the development stage at which they are likely to be collected during vegetation dragging and reflect a complex interaction between ticks, their hosts and the environment.

Introduction

Many studies have examined the association between ticks, their hosts and the environment, but most have been of relatively short duration (typically 1–2 years) and there is little information on longer-term changes in tick populations. In earlier publications (Horak, Gallivan & Spickett 2011; Spickett, Gallivan & Horak 2011) we described changes in the numbers of questing ticks and the population dynamics of the four major tick species, *Amblyomma hebraeum*, *Rhipicephalus appendiculatus*, *Rhipicephalus decoloratus* and *Rhipicephalus zambeziensis*. The questing ticks were collected monthly by dragging flannel strips over the vegetation at two sites in the Kruger National Park (KNP) over a period of 164 months. In the present publication we describe changes in the numbers of the less commonly collected species, namely *Amblyomma marmoreum*, *Dermacentor rhinocerinus*, *Haemaphysalis elliptica*, *Hyalomma truncatum*, *Rhipicephalus evertsi evertsi*, *Rhipicephalus simus* and *Rhipicephalus turanicus*.

Materials and methods

The KNP is a large nature reserve of nearly 2 million ha in north-eastern South Africa. Five vegetation types (Acocks 1988) and 35 Landscape Zones (Gertenbach 1983) have been identified in the reserve. The study sites at Skukuza and Nhlowa Road and the associated climate, methods of tick collection and statistical analyses have been described in detail by Horak *et al.* (2011). The climate in the southern KNP is described as tropical with summer rainfall. Annual rainfall is measured from June to May; consequently, we have chosen June to represent the commencement of each year.

Briefly, questing ticks were collected monthly by drag-sampling the vegetation with flannel strips (Spickett *et al.* 1992) at two sites in the KNP, namely Nhlowa Road and Skukuza. The Nhlowa Road site was in Landscape Zone 17, which has been described as a *Sclerocarya caffra* – *Acacia nigrescens* savanna, and the Skukuza site in Landscape Zone 4 (Thickets of the Sabie and Crocodile Rivers).

Three drags, approximately 250 m long and 1 m wide, were made at a normal walking speed in each of three visually selected habitats (grassland, woodland and gully) at each site. In addition to the flannel strips, the operator responsible for dragging the strips also wore flannel leggings. Because of the limited number of gullies at each site, the same gullies were usually sampled every month, whereas the sampling locations in grassland and woodland usually varied from month to month. After each drag the ticks on the flannel strips and the leggings were removed using sharp-pointed forceps and stored in 70% ethyl alcohol in internally labelled, plastic-stoppered glass vials for later identification and quantification.

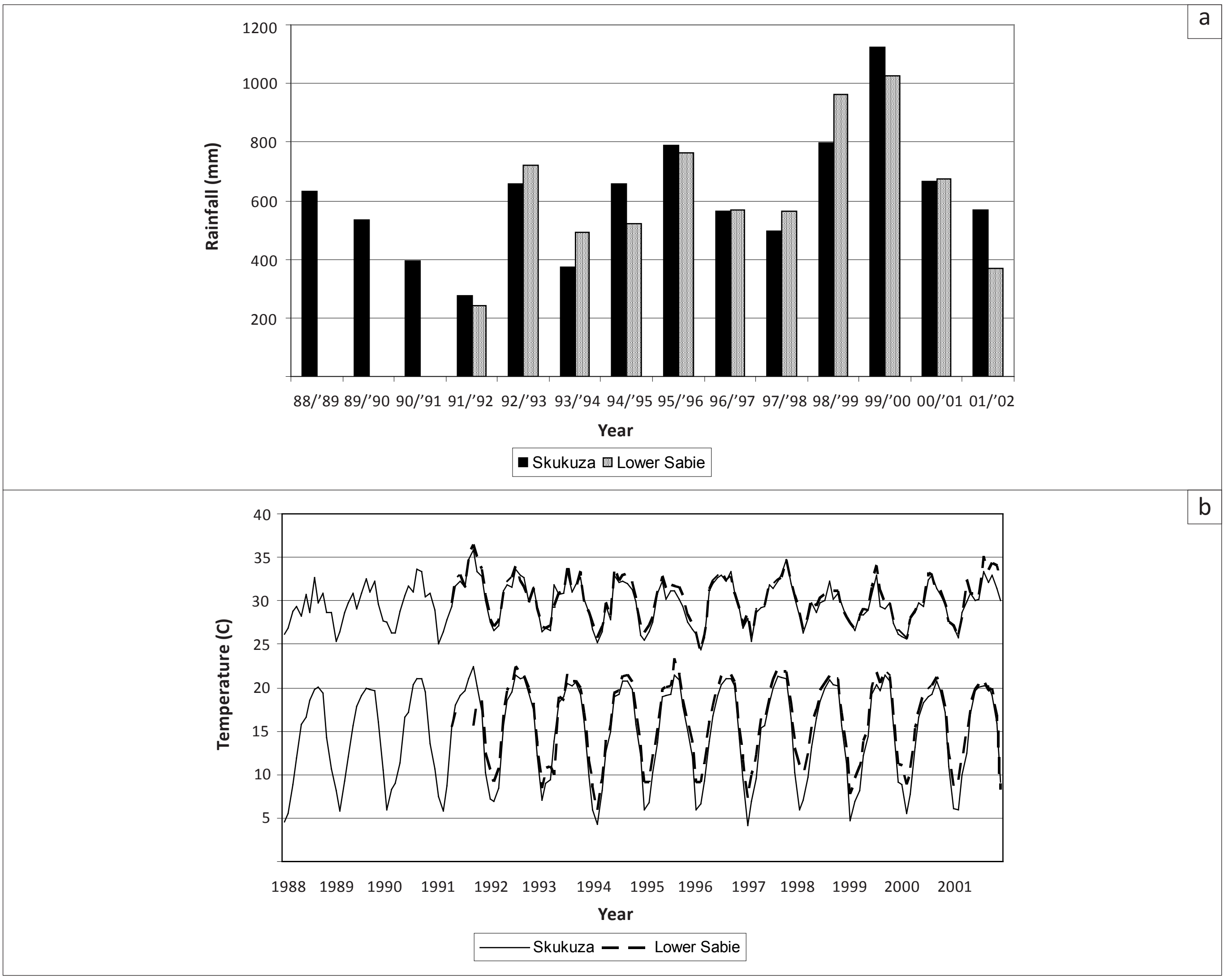
Sampling commenced in August 1988 and continued in every habitat at the two localities until March 2002, except after heavy rainfall, during a bush fire or upon sighting elephants (*Loxodonta africana*), African buffaloes (*Syncerus caffer*) or lions (*Panthera leo*) in the vicinity.

The identification of the immature stages of ticks, particularly of the lesser-known species, can be a difficult and time-consuming exercise. The larvae and nymphs of *A. marmoreum* have been described by Theiler and Salisbury (1959), those of *D. rhinocerinus* by Keirans (1993), of *Ha. elliptica* by Apanaskevich, Horak and Camicas (2007), of *Hy. truncatum* by Apanaskevich and Horak (2008), and of the various *Rhipicephalus* species by Walker, Keirans and Horak (2000).

Results and discussion

Annual rainfall (June–May) at the Skukuza rest camp averaged 609 mm over the period of the study, with a range of 275 mm – 1122 mm (Figure 1a). Average annual rainfall at the Lower Sabie rest camp, the closest climate station to the Nhlowa Road site, was similar to that at Skukuza. Mean monthly maximum temperatures fluctuated around 33 °C in mid-summer, while minimums rarely fell below 5 °C in winter (Figure 1b).

The numbers of all species collected from the vegetation are summarised in Table 1. Four taxa could be identified only to a generic level, including 188 *Amblyomma* sp. larvae, 104 *Haemaphysalis* sp. larvae, a single *Ixodes* sp. nymph and a single *Rhipicephalus pravus* group larva. Counts of specimens of these four taxa and those of the four major tick species,



[a], weather readings only commenced during 1991 at Nhlowa Road.

FIGURE 1: (a) Annual rainfall (June–May) and (b) mean monthly maximum and minimum temperatures at Skukuza and Lower Sabie[a], during the study period.

namely *A. hebraeum*, *R. appendiculatus*, *R. decoloratus* and *R. zambeziensis* are listed collectively as 'other species' in the table. Population dynamics of the four major tick species have been discussed in earlier publications (Horak *et al*. 2011; Spickett *et al*. 2011). Except for *Ha. elliptica*, *R. simus* and *R. turanicus*, of which adults were the most commonly collected stage, larvae were the most commonly collected stage of all these tick species.

Amblyomma marmoreum

Leopard tortoises (*Geochelone pardalis*), the largest tortoise species in South Africa (Branch 1998), are the preferred hosts of the adults of *A. marmoreum* and hence it is colloquially known as the South African tortoise tick (Horak *et al*. 2006a). Adult ticks are rarely found on hosts other than reptiles, but the larvae infest a wide range of hosts, including carnivores, herbivores, hares, birds and reptiles (Horak *et al*. 2006a).

Amblyomma marmoreum larvae were collected more frequently at Skukuza than at Nhlowa Road ($p < 0.001$) and accounted for 98.8% of the *A. marmoreum* specimens collected (Table 1). The riverine thickets at Skukuza probably afforded greater protection for younger tortoises against predators and this may explain why larvae were collected more frequently at Skukuza than at Nhlowa Road. The collections were seasonal ($p < 0.001$), with most larvae collected between March and July. There was a definite peak in May at Skukuza but not at Nhlowa Road (Figure 2a). This corresponds to the seasonality of *A. marmoreum* larvae on greater kudus (*Tragelaphus strepsiceros*), impalas (*Aepyceros melampus*), scrub hares (*Lepus saxatilis*) and helmeted guineafowls (*Numida meleagris)* examined in the KNP (Horak *et al*. 1991; Horak *et al*. 1992; Horak *et al*. 1993; Horak *et al*. 1995; Horak *et al*. 2003), and countrywide on leopard tortoises (Horak *et al*. 2006a).

Although there was considerable year-to-year variability, the numbers of *A. marmoreum* larvae collected each year appeared to decline from 1990 to 2001 (Figure 2b). The size of the collections was not significantly correlated with annual rainfall or rainfall over the activity period (February–September). The numbers did not differ significantly among habitats ($p = 0.20$), but there was a trend towards more frequent collections in the gullies than in grassland and woodland (Table 2). The slightly more frequent collections of *A. marmoreum* larvae in gullies could imply that tortoises prefer to browse on the more succulent vegetation usually found there.

Dermacentor rhinocerinus

Adult *D. rhinocerinus* are found almost exclusively on black and white rhinoceroses (*Diceros bicornis* and *Ceratotherium simum*) (Keirans 1993), of which nearly all in the southern KNP are infested and on which the tick may occur in large numbers (Knapp *et al*. 1997). Adult ticks quest for their preferred hosts at a height of 1 m or more on thick-stemmed, tall grass species (Horak, personal observations 2000). They are seldom picked up on flannel strips and only two adults were collected (Table 1). Because adult ticks have a very strong affinity to rhinoceroses they have not been collected from any of the numerous host species we examined in the KNP. It is this affinity that probably makes the operator dragging the flannel strips and the strips themselves unattractive to the ticks.

The rodent hosts of the immature stages have been detected only recently (Horak & Cohen 2001). In Mthethomusha Nature Reserve (adjacent to the KNP and where there are also white rhinoceroses) three rodent species, namely bushveld gerbils

TABLE 1: Numbers of the less common tick species collected by dragging at the Skukuza and Nhlowa Road sites in the Kruger National Park (August 1988–March 2002).

Species	Stage	Skukuza (Zone 4)		Nhlowa Road (Zone 17)	
		N	%	*N*	%
Amblyomma marmoreum	LL	1604	1.27	249	0.12
	NN	6	< 0.01	3	< 0.01
Dermacentor rhinocerinus	LL	2	< 0.01	5	< 0.01
Haemaphysalis aciculifer	AA	–	–	2	< 0.01
	LL	2	< 0.01	14	0.01
Haemaphysalis hoodi	AA	1	< 0.01	–	–
Haemaphysalis elliptica	LL	37	0.03	23	0.01
	NN	5	< 0.01	5	< 0.01
	AA	198	0.16	363	0.17
Hyalomma truncatum	LL	14	0.01	10	0.005
	AA	3	< 0.01	2	< 0.01
Rhipicephalus evertsi evertsi	LL	1299	1.03	3921	1.85
	NN	1	< 0.01	–	–
	AA	1	< 0.01	2	< 0.01
Rhipicephalus maculatus	NN	–	–	1	< 0.01
Rhipicephalus simus	LL	83	0.07	13	< 0.01
	NN	1	< 0.01	–	–
	AA	323	0.26	354	0.17
Rhipicephalus turanicus	LL	1	< 0.01	4	< 0.01
	AA	2	< 0.01	127	0.06
All other species	LL, NN, AA	122 227	97.16	206 471	97.59
Total	–	**125 810**	–	**211 569**	–

N, number of ticks collected; %, percentage of the number of ticks collected at the site.
LL, larvae; NN, nymphs; AA, adults.

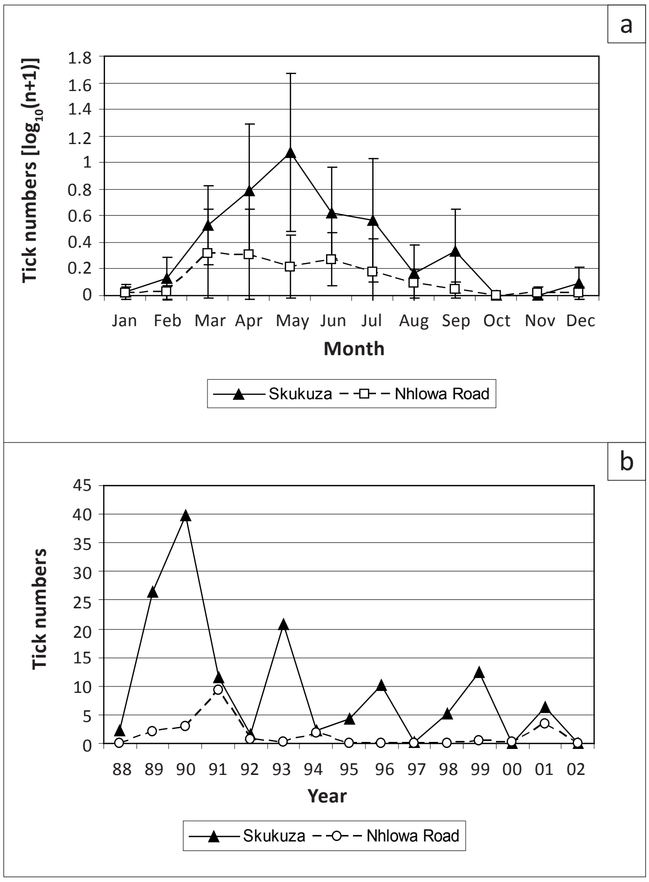


FIGURE 2: (a) Mean collections of *Amblyomma marmoreum* larvae (mean ± 95% confidence interval) per month and (b) mean monthly collections per year at Nhlowa Road and Skukuza.

(*Tatera leucogaster*), red veld rats (*Aethomys chrysophilus*) and Natal multimammate mice (*Mastomys natalensis*) were found infested with the immature stages of *D. rhinocerinus* (Horak & Cohen 2001). The small size of these animals implies that the immature stages of *D. rhinocerinus* quest for hosts from the soil surface rather than the vegetation, and only seven larvae were collected from the flannel strips (Table 1). No bushveld gerbils or red veld rats examined in the KNP were infested (Braack *et al*. 1996).

Haemaphysalis elliptica

Haemaphysalis elliptica is an old taxon – originally described by Koch around the Cape of Good Hope in the nineteenth century – and has recently been reinstated as a valid species (Apanaskevich *et al*. 2007). All reports of *Ha. leachi* in South Africa from before 2007 are, in fact, incorrect and should actually refer to *Ha. elliptica*, as *Ha. leachi* does not occur in this country (Apanaskevich *et al*. 2007).

Adult ticks were the most commonly collected stage of *Ha. elliptica*. In the KNP adult ticks have most often been collected from the larger felids, such as lions, leopards (*Panthera pardus*), cheetahs (*Acinomyx jubatus*) and African civets (*Civettictis civetta*). They have also been recovered from African wild cats (*Felis silvestris*) and feral cats (*Felis cattus*), black-backed jackals (*Canis mesomelas*), wild dogs (*Lycaon pictus*) and spotted hyaenas (*Crocuta crocuta*) (Horak *et al*. 1987; Horak *et al*. 2000a). The immature stages are usually found on rodents (Braack *et al*. 1996; Horak, Fourie & Braack 2005), but small numbers may also infest carnivores, scrub hares and helmeted guineafowls (Horak *et al*. 1987; Horak *et al*. 1991; Horak *et al*. 1993; Horak *et al*. 1995; Horak *et al*. 2000a). Very few larvae or nymphs were collected from the vegetation (Table 1). However, as their preferred hosts are rodents, they probably quest for these from the soil surface and do not attach to flannel strips dragged over the vegetation.

Haemaphysalis elliptica adults were more commonly collected at Nhlowa Road than at Skukuza ($p = 0.001$). Landscape Zone 17 is at the centre of lion activity in the KNP (Gertenbach 1983), which may account for the greater number of adult ticks in this area. There was a significant difference between the numbers of adults collected over years ($p < 0.001$). Some were collected from 1988 to 1990, but few were collected from 1991 to 1993. The numbers then increased, with a marked peak in 2000 (Figure 3a). The patterns were similar at both sites, but there was a significant year-by-site interaction ($p < 0.001$), because more were collected at Skukuza in 1988 and 1989 while more were collected at Nhlowa Road in the other years. The collections of adult ticks were correlated with annual rainfall of the preceding year at both sites ($r > 0.67$; $p < 0.01$). A significant correlation with rainfall 2 years before was also observed at Skukuza ($p = 0.64$; $p < 0.05$), and a positive but non-significant correlation with rainfall observed at Nhlowa road ($p = 0.48$; $p < 0.2$). The dramatic increase in numbers in 1999 and 2000 followed 2 years of above-average rainfall in 1998 and 1999. Following a rodent explosion in 1993 (Horak, Spickett & Braack 2000b), after above-average annual rainfall in 1992, numbers peaked slightly at Nhlowa Road in 1994 and 1995. The increase in numbers of *Ha. elliptica* adults around the turn of the century was probably also associated

TABLE 2: Mean monthly tick collections [log$_{10}$(n + 1)] by habitat.

Species	Stage	Combined			Skukuza (Zone 4)			Nhlowa Road (Zone 17)		
		grassland	gully	woodland	grassland	gully	woodland	grassland	gully	woodland
Amblyomma marmoreum	LL[1]	0.164	0.225	0.146	0.281	0.327	0.233	0.054	0.128	0.064
Haemaphysalis elliptica	AA	$0.102^{a,b}$	0.139^{a}	0.088^{b}	0.094	0.101	0.069	0.109^{a}	0.174	0.106^{a}
Rhipicephalus evertsi evertsi	LL	0.468^{a}	0.244	0.454^{a}	0.253	0.171	0.322	0.669^{a}	0.313	0.578^{a}
Rhipicephalus simus	AA[2]	0.076^{a}	0.240^{c}	0.145^{b}	0.105^{a}	0.224^{b}	$0.179^{a,b}$	0.049^{a}	0.255	0.115^{a}
Rhipicephalus turanicus	AA[3]	–	–	–	–	–	–	$0.096^{a,b}$	0.181^{a}	0.034^{b}
Total number of ticks collected		**2.049^{a}**	**2.139^{a}**	**2.301**	**1.923^{a}**	**$2.073^{a,b}$**	**2.229^{b}**	**2.168**	**2.202**	**2.369**

Habitats with the same superscripted letter within a site are not significantly different ($p < 0.05$).
Numbered superscripts denote the period of collection: [1], Mar–Sep; [2], Oct–Jun; [3], Jan–Jun.
LL, larvae; AA, adults.

with an increase in rodent populations during a period of above-average rainfall.

According to the time series assessment, the seasonality of *Ha. elliptica* adults was not statistically significant, probably because of the small numbers collected in most years. However, an ANOVA showed a significant difference between months ($p < 0.001$), with the largest numbers collected in late summer and autumn (February–June) and the smallest numbers in spring (September–November) (Figure 3b). A similar pattern was observed at both sites. There are no data regarding the seasonality of adult *Ha. elliptica* on carnivores in the KNP, but in north-eastern KwaZulu-Natal, south-east of the KNP, adult ticks on dogs in rural communities were found mostly from January to March or April (Horak, Emslie & Spickett 2001).

Haemaphysalis elliptica larvae were more commonly collected at Skukuza than at Nhlowa Road. Most larvae were collected in 1989 and 1990, and only sporadically thereafter. The largest numbers were collected in September and November, and only two of the 60 were collected between January and April. Nymphs were collected sporadically in the early 1990s and again towards the turn of the century. Eight of the 10 nymphs were collected between July and October. The September–November and July–October peaks for collections of *Ha. elliptica* larvae and nymphs, respectively, correspond to the seasonal peaks in *Ha. elliptica/spinulosa* larval and nymphal infestations on red veld rats in the southern KNP (Braack *et al*. 1996).

As shown in Table 2, the largest numbers of *Ha. elliptica* adults were collected in the gullies, while fewest were collected in woodland ($p < 0.01$). This pattern was consistent over months and at both sites. However, there was a significant difference between years ($p = 0.02$), with the largest numbers collected in the gullies until the late 1990s (Figure 3c) followed by more frequent collections in grassland and woodland. Eight of the ten nymphs were collected in the gullies.

Tall grasslands appear to support a higher diversity of small mammal populations (Monadjem 1997), but many of the rodent hosts of the immature stages of *Ha. elliptica* prefer sheltered, rocky areas (Skinner & Smithers 1990). During periods of below-average rainfall, when grass swards were shorter and ground cover was reduced, gullies were probably the preferred habitat of many of the rodent hosts. Around the turn of the century the majority of *Ha. elliptica* adults were collected in grassland and woodland. Denser ground cover and taller grass swards following a period of higher rainfall would have provided a more suitable habitat for many rodent species, and an increase in rodent populations would have led to an expansion of habitat use. Thus, the population dynamics and habitat distribution of questing *Ha. elliptica* are probably determined by the effects of rainfall on the populations of rodent hosts of the immature stages, rather than the carnivore hosts of the adults.

Hyalomma truncatum

Although only 24 larvae and five adult *Hy. truncatum* were collected from the vegetation (Table 1), these low numbers should not be regarded as a reflection of actual abundance of this tick in the KNP. During the first 6 years of this survey, five scrub hares were examined monthly around Skukuza, and the 360 examinations during this time yielded a total of 36 647 larvae and 9896 nymphs of this two-host tick (Horak

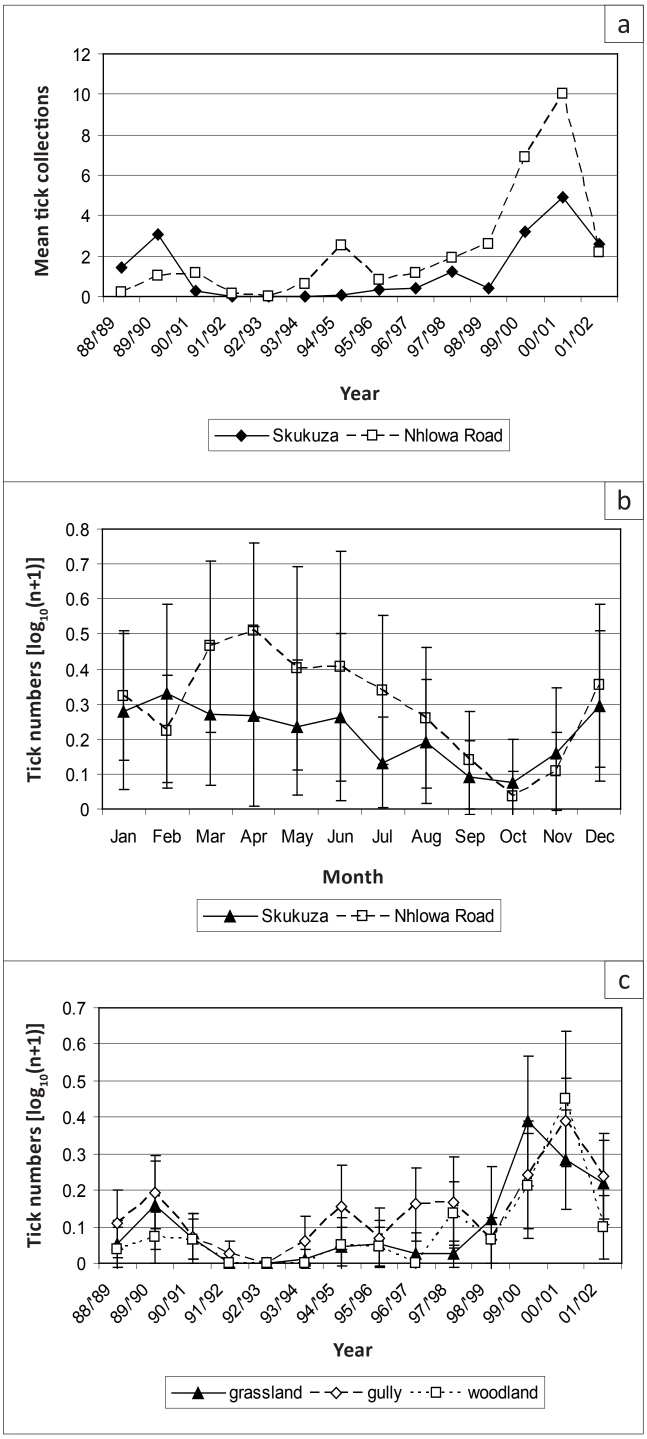


FIGURE 3: (a) Mean monthly collections of *Haemaphysalis elliptica* adults from each site per year, (b) mean collections (± 95% confidence interval) per month from each site and (c) mean collections (± 95% confidence interval) from each habitat per year.

et al. 1993; Horak *et al*. 1995). Adult *Hy. truncatum* have been collected from the large browsers and grazers in the KNP, including giraffes (*Giraffa camelopardalis*), Burchell's zebras (*Equus burchellii*), elands, (*Taurotragus oryx*), white rhinoceroses and kudus, as well as warthogs (*Phacochoerus africanus*) (Horak, De Vos & De Klerk 1984; Horak *et al*. 1988; Horak *et al*. 1992; Horak, Golezardy & Uys 2007; Knapp *et al*. 1997). The discrepancy between the numbers collected by dragging and the numbers on scrub hares strongly suggests that *Hy. truncatum* larvae quest for hosts from the soil surface. The adults definitely quest for hosts from the soil surface and can readily be seen scuttling along the ground towards any large potential host.

Rhipicephalus evertsi evertsi

Rhipicephalus evertsi evertsi is a two-host tick that infests a wide range of host species (Walker *et al*. 2000). In the KNP, Burchell's zebras and giraffes appear to be preferred hosts for all stages (Horak *et al*. 1984; Horak *et al*. 2007), while impalas and scrub hares are important hosts for the immature stages (Horak *et al*. 1993; Horak *et al*. 1995; Horak *et al*. 2003). Larvae were most commonly collected during dragging (Table 1) and, theoretically, only larvae and adults should quest for hosts. The single nymph that was collected had probably become dislodged just before or after moulting and was questing for a host. Very few adults were collected, probably because they quest for hosts from the soil surface or, like the adults of many species, they do not attach to flannel strips.

In previous drag-sampling studies in Landscape Zones 4 and 17 there was no evidence of seasonality in the numbers of questing *R. evertsi evertsi* larvae collected (Spickett *et al*. 1992; Horak *et al*. 2006b). The present study, however, showed significant periodicity at both sites ($p < 0.001$). At Nhlowa Road there were two annual peaks (November–February and June–July), whereas at Skukuza, there was only a single peak (November–December) with a nadir between May and June (Figure 4a). Based on the development times seen in the laboratory, *R. evertsi evertsi* can complete more than one life cycle annually at the prevailing temperatures in the KNP (Horak *et al*. 2003). At Nhlowa Road the summer and winter peaks correspond to those observed on Burchell's zebras (Horak *et al*. 1984), suggesting that the seasonal pattern was related to the pattern of zebra migration. At Skukuza, the late spring peak and late autumn nadir differed not only from the pattern observed in other drag-sampling studies but also from that observed on impalas and scrub hares in this landscape zone (Horak *et al*. 1993; Horak *et al*. 2003). The reasons for the differences between the seasonal patterns observed in the present study and previous studies are unknown. They may be related to seasonal differences in habitat use by ungulates within Landscape Zone 4, or they may be because of the relatively short duration of the sampling periods (1–4 years) in the earlier studies. In the present study there was considerable variability among years and the general seasonal pattern was seen only over the longer time period.

The numbers of *R. evertsi evertsi* larvae collected differed significantly among years ($p < 0.001$) and there was a significant year-by-site interaction ($p = 0.028$), with proportionally greater changes at Skukuza than at Nhlowa Road. However, the trends were similar at both sites, with peaks in the early 1990s, a decline through the mid-1990s, and subsequent increases in the late 1990s. Numbers declined in 2000 (Figure 4b). The numbers were not significantly correlated with seasonal rainfall at either site. The apparent differences in the annual trends at the two sites may be related to differences in the host communities. The populations of the larger ungulates at Nhlowa Road, such as zebras and giraffes, appear to be less sensitive to changes in rainfall (Ogutu & Owen-Smith 2005) than the populations of smaller ungulates, such as impalas, at Skukuza.

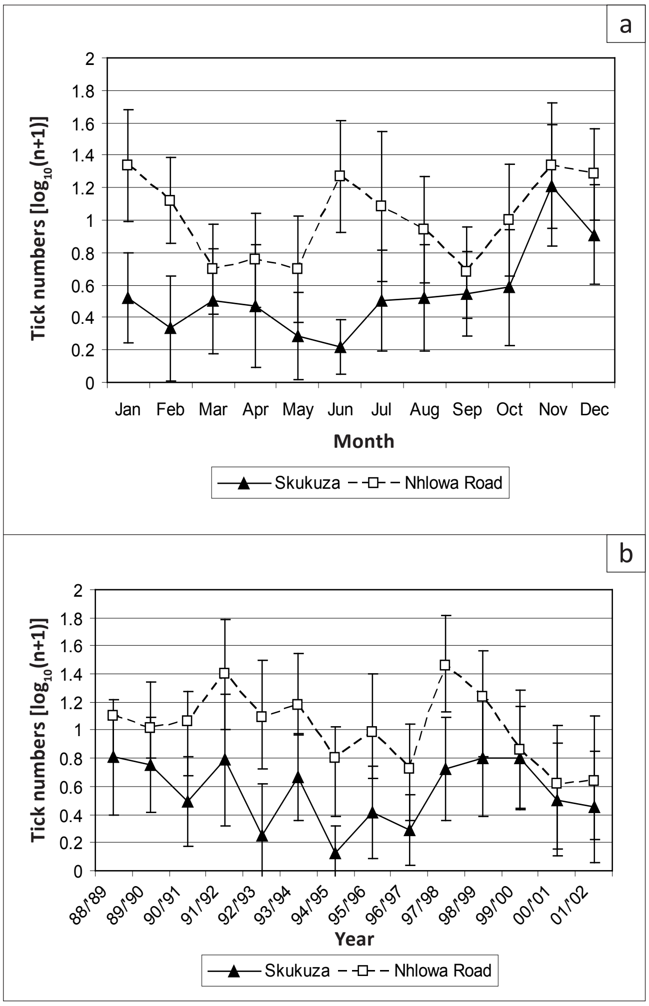


FIGURE 4: Mean collections (± 95% confidence interval) of *Rhipicephalus evertsi evertsi* larvae (a) by month and (b) by year at the two sites.

Larvae were more commonly collected at Nhlowa Road than at Skukuza ($p < 0.001$) and there was a significant habitat-by-site interaction ($p = 0.002$). At Nhlowa Road, larvae were least frequently collected in the gullies and most commonly in the grassland (Table 2), probably because of the large numbers of zebras and other grazers at this locality. At Skukuza, *R. evertsi evertsi* larvae were most commonly collected in the woodland, probably because of the presence of large numbers of impalas and other browsers, but the difference among habitats was not statistically significant ($p > 0.1$). The differences among habitats were not significant among months or years ($p > 0.4$).

Rhipicephalus simus

Adults were the most commonly collected stage of *R. simus*. The preferred hosts of adult *R. simus* are large ruminants, such as African buffaloes, and monogastric animals, such as large carnivores, warthogs, zebras and rhinoceroses (Walker *et al*. 2000). Large numbers of *R. simus* adults have been collected from lions, leopards, warthogs, Burchell's zebras and white rhinoceroses in the KNP (Horak *et al*. 1984; Horak *et al*. 1988; Horak *et al*. 2000a; Knapp *et al*. 1997).

The collections of *R. simus* were seasonal, with a peak between February and March and a nadir between August and September (Figure 5a). The numbers did not differ significantly between the two sites ($p = 0.2$) and the seasonal patterns were similar. The peak in adult numbers corresponds with that on Burchell's zebras and warthogs in the KNP (Horak *et al*. 1984; Horak *et al*. 1988) and on warthogs in Swaziland in a *Sclerocarya caffra* – *Acacia nigrescens* savanna (Gallivan & Surgeoner 1995).

There was a significant difference between the numbers of *R. simus* adults collected over the years ($p < 0.001$). Numbers declined from 1988 to 1991, then increased again in 1994, followed by a peak in 2000 (Figure 5b). The trends differed significantly between the two sites ($p < 0.001$). At Skukuza, numbers tended to be higher between 1988 and 1989 than from 1997 to 2000. However, at Nhlowa Road the numbers of *R. simus* adults were higher from 1993 to 1995, with a marked peak in 1994.

The numbers of adult *R. simus* collected at Skukuza were significantly correlated with annual rainfall during the 2 previous years ($p < 0.05$). At Nhlowa Road, the numbers were significantly correlated with rainfall 2 years before ($p = 0.05$), but not with that of the preceding year. The decline in numbers in the early 1990s corresponded to a period of decreasing annual rainfall and to a marked decline in the warthog population in the KNP (Ogutu & Owen-Smith 2005). The decline in annual rainfall probably also caused a decline in the populations of rodents, which are the preferred hosts of the immature stages of this tick (Braack *et al*. 1996; Horak *et al*. 2005; Norval & Mason 1981; Petney *et al*. 2004).

Following a period of above-average rainfall in 1992, there was an eruption of rodent populations in 1993 (Horak *et al*. 2000b) that may have accounted for the large number of adult *R. simus* collected at Nhlowa Road during 1994. As with the adults of *Ha. elliptica*, the increase in the numbers of *R. simus* adults around the turn of the century was probably associated with an increase in rodent populations during a period of above-average rainfall.

As shown in Table 2, adult *R. simus* were most commonly collected in the gullies and least frequently in the grassland ($p < 0.001$). There was a significant difference in the habitat distribution between the two sites ($p = 0.03$). At Skukuza, 48.3% of the ticks were collected in the gullies and 16.4% in grassland, whereas at Nhlowa Road, 69.2% were collected in the gullies and only 7.6% in grassland. Habitat distribution

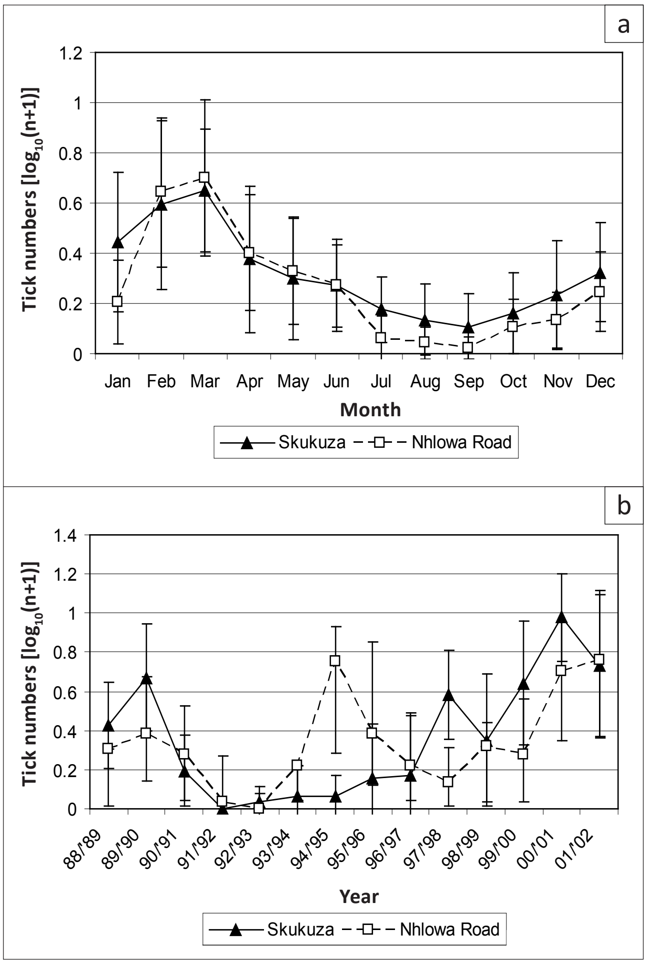


FIGURE 5: Mean collections (± 95% confidence interval) of *Rhipicephalus simus* adults (a) by month and (b) by year at Nhlowa Road and Skukuza.

differed significantly among months ($p = 0.025$), with the most pronounced difference during February and March, the period of peak activity. There was also a marginally significant difference in habitat distribution among years ($p = 0.1$), with highest numbers in the gullies; however, in 2000 the numbers were marginally higher in woodland. As in the case of *Ha. elliptica*, the habitat distribution probably corresponds to the pattern of habitat use by the hosts of the immature stages.

Rhipicephalus simus larvae were more frequently collected at Skukuza than at Nhlowa Road. Almost half (45.8%) were collected in 1989, while the second largest collection (14.6%) was made in 2001. Other collections were sporadic. At Skukuza, most *R. simus* larvae were collected from January to June, but at Nhlowa Road most were collected from June to November. At Skukuza, more larvae were collected in the gullies than in grassland, whereas at Nhlowa Road, most larvae were collected in woodland.

Rhipicephalus turanicus

Adult *R. turanicus* have been collected from lions, leopards, cheetahs, African wild dogs, feral cats and scrub hares in the KNP, but none of the animals were heavily infested (Horak *et al*. 1993; Horak *et al*. 1995; Horak *et al*. 2000a). No immature stages have been collected from animal hosts within the

KNP or adjacent nature reserves. Scrub hares examined on farms around Hluhluwe in north-eastern KwaZulu-Natal were infested with all stages of *R. turanicus* (Horak *et al.* 1995) and crested francolins (*Francolinus sephaena*) on a farm in Limpopo were infested with larvae (Uys & Horak 2005). Adult ticks were also common on dogs in Maputo Province, Mozambique, adjacent to the KNP (Neves, Afonso & Horak 2004).

Rhipicephalus turanicus was most commonly collected at Nhlowa Road (97.8%) and adults were the most commonly collected stage (Table 1). As mentioned before, Landscape Zone 17 is at the centre of lion distribution within the KNP (Gertenbach 1983) and the herds of large grazers would support populations of other carnivores. Collections were seasonal ($p < 0.001$), with a peak between February and March (Figure 6a). There were significant differences between the numbers collected among years ($p = 0.002$), with peaks in 1991, 1994, 1995, 1999, 2001 and 2002 (Figure 6b). The numbers of *R. turanicus* adults were not correlated with rainfall and, as shown in Table 2, ticks of this stage were collected in the gullies more often than in woodland ($p < 0.001$). This pattern was consistent among years and months.

There was a strong correlation ($r = 0.7$; $p = 0.009$) between the numbers of adult *R. simus* and adult *R. turanicus* collected annually at Nhlowa Road. The year-to-year patterns of the two species were similar and both species were most commonly collected in the gullies. However, woodland yielded the fewest *R. turanicus* adults, whereas the grassland yielded the fewest *R. simus* adults. The distribution of adult *R. turanicus* among habitats and year-to-year collection patterns were also similar to those of adult *Ha. elliptica* at the Nhlowa Road site.

Conclusion

In order to determine the population dynamics of free-living ixodid ticks, questing ticks were collected monthly for 164 months from the vegetation at two localities in the KNP. Of the collected species, 14 could be identified to specific level. Larvae of *A. marmoreum* and *R. evertsi evertsi*, and adults of *Ha. elliptica*, *R. simus* and *R. turanicus* were collected in sufficient numbers to conclude that they quest for hosts from the vegetation. The host-seeking strategies of their remaining developmental stages and those of the tick species collected only in small numbers still need to be investigated.

The value of long term sampling at more than one locality and within various habitats at each locality yielded several answers and posed a number of questions. Should more samples be taken within the predominant habitat at a locality, for example in the thickets and woodlands of a thicket locality and in the grasslands of a savanna locality, to obtain more accurate results pertaining to an entire locality? What are the reasons for markedly more numerous questing ticks in a treed savanna locality compared with a locality composed largely of thickets? What value can be added by simultaneously sampling the major host species within a

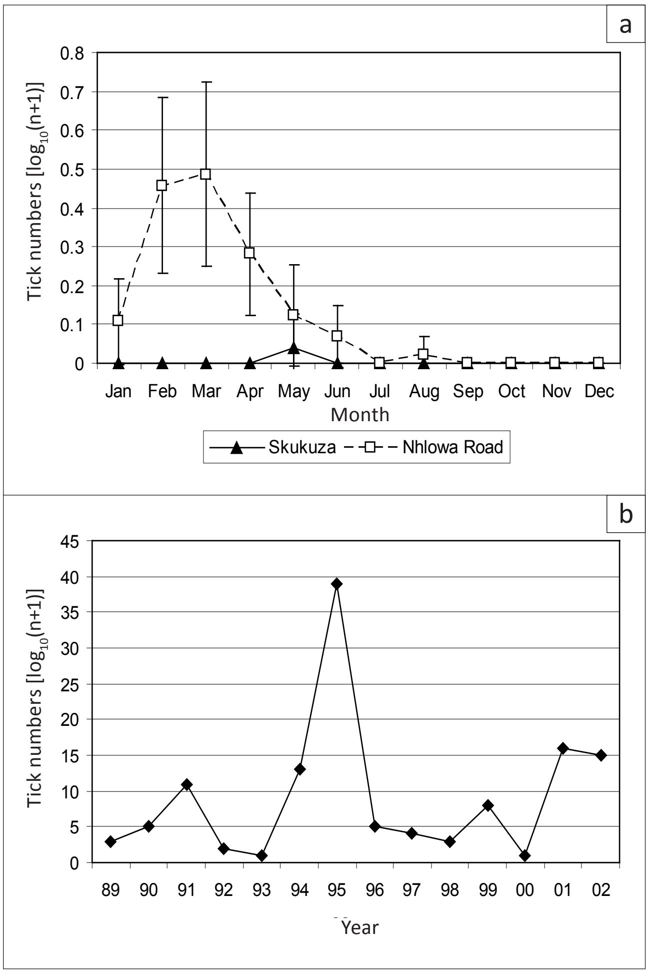


FIGURE 6: (a) Mean collections (± 95% confidence interval) of *Rhipicephalus turanicus* adults by month at the two sites and (b) total collections by year at Nhlowa Road.

study site for ticks and determining host densities and daily and seasonal movements?

Finally, logistical challenges to what can be achieved in the field in a large nature reserve need to be considered, for example (1) the dangers posed to field workers by large predators, African buffaloes, rhinoceroses and elephants, (2) the number of drag samples that can be accomplished in a day to ensure reasonable homogeneity, as the total length of the drags placed end to end covered a distance of 2250 m at each locality, and (3) the number of people, besides an armed ranger, needed to collect, within a reasonable time frame, the thousands of ticks sometimes collected in a single drag.

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