Effect of burning on the numbers of questing ticks collected by dragging

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ABSTRACT

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Sixteen experimental burn plot replicates, in groups of four, in four landscape zones of the Kruger National Park, South Africa, and from which wildlife are not excluded, have been subjected to fixed, regular burning regimens since 1954. In 1999, a study to determine the effect of burning on ixodid ticks questing for hosts from the vegetation of the plots was initiated, and six sub-plots, with identical histories, within each of two of the burn plot replicates in *Combretum collinum/Combretum zeyheyri* woodland on granite, were selected. With few exceptions these 12 sub-plots, as well as unburned vegetation adjacent to each of the replicates, were sampled for ticks at monthly intervals for a period of 39 months by dragging with flannel strips. The existing regimen of burning during August or during October on individual sub-plots was continued during this time. A total of 14 tick species was recovered from the plots of which nine could be considered major species. Sufficient numbers for statistical analysis of only eight species were, however, collected. Burning appeared to have little short-term effect on the number of ticks recovered. In the longer term, the response varied from no change, an increase, or a decrease in the numbers of ticks collected each year after burning. Tick species, life cycle, seasonality, questing strategy, host preference and host utilization of the habitat were important determinants of the effect of burning.

Keywords: Experimental burn plots, fire, *Amblyomma hebraeum*, *Amblyomma marmoreum*, *Haemaphysalis leachi*, *Rhipicephalus appendiculatus*, *Rhipicephalus (Boophilus) decoloratus*, *Rhipicephalus evertsi evertsi*, *Rhipicephalus simus*, *Rhipicephalus zambeziensis*

INTRODUCTION

The Kruger National Park, located in the Lowveld of north-eastern South Africa, is approximately 1.9 million ha in size and has been managed as a wildlife conservation area since its proclamation in 1926. In 1954, during a period of fire suppression within the park, a burn plot experiment was launched. The history and a description of the experimental burn plots have been recorded by Trollope, Potgieter, Biggs & Trollope (1998) and are briefly repeated here. The experiment was initially designed to obtain an understanding of the effects of season and frequency of burning on vegetation, and was conducted in four major veld types of the park, in each of which four separate replicates were laid out. Each replicate is approximately 100 ha in extent and comprises 11 to 13 treatment sub-plots and an un-burned control, each approximately 7 ha in size, in a contiguous rib-

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bon-like spatial design. Essentially unaltered burning regimens have been applied and monitored on the various treatment plots until the present. Recently, however, projects to determine the effect of burning on a wider range of elements than just the vegetation were initiated, and small mammals, reptiles, birds, insects and ixodid ticks were included.

Surveys on the seasonality of ticks infesting animals in the park were conducted intermittently between 1978 and 1994 by examining various species at monthly intervals for periods ranging from 13 to 72 consecutive months (Horak 1998). A survey on the seasonality and species diversity of ticks questing for hosts from the vegetation was initiated in 1988 (Horak, Spickett & Braack 2000b). In the latter study ticks were collected at approximately monthly intervals for 164 consecutive months, by dragging flannel strips over the vegetation of two landscape zones in the south of the park. In September 1988 part of the vegetation in one of the zones was subjected to a controlled total burn and the effect of this fire on the numbers and seasonality of questing ticks was determined (Spickett, Horak, Van Niekerk & Braack 1992). Tick numbers were reduced after the burn, but increased after varying periods thereafter depending on tick species, patterns of seasonal occurrence, and host preference.

As part of the initiatives to make greater use of the experimental burn plots and in view of our ongoing involvement in tick research in the park we were invited to determine the effect of burning on the numbers of ticks questing from the vegetation in the experimental burn plots. This report records the monthly tick counts in sub-plots within two replicates of the experimental burn plots before and after burns as well as on unburned vegetation adjacent to the replicates over a period of 39 consecutive months.

MATERIALS AND METHODS

Three of four experimental burn plot replicates are located just north and one just south of the road between the tourist rest camps of Skukuza and Pretoriuskop, and two of the northerly replicates were selected for drag-sampling (Fig. 1). The sub-plots in the more westerly replicate have for convenience been identified as the Nwaswitshaka burn plots (25°08' S; 31°38' E), while those in the more easterly replicate are referred to as the Skukuza burn plots (25°10' S; 31°44' E). Both sets of replicates are in a landscape zone described as *Combretum collinum*/*Combretum zeyheyri* woodland on granite (Zone 3A: Gertenbach 1983).

Each replicate is surrounded by an approximately 4 m wide fire-break, which is kept reasonably free of vegetation by means of a road-grader, and is subdivided by similar fire-breaks into 12 sub-plots, each approximately 7 ha in size. Wildlife has free access to all the experimental burn plot replicates. The sub-plots within the Nwaswitskaka and Skukuza experimental burn plot replicates are paired and at the commencement of the survey the sub-plots of each pair had been subjected to the same burning regimen for the previous 45 years. Six sub-plots that had received the same treatment were selected at each locality. One sub-plot was not burned (control), a second was burned the first week of August each year, a third sub-plot was burned the first week of August every second year, a fourth was burned the first week of August every third year, a fifth sub-plot was burned the first week of October every second year, and a sixth was burned the first week of October every third year. Unburned vegetation adjacent to the fire-break surrounding the 12 sub-plots comprising the burn plot replicate was selected as a second control. As chance would have it the experi-

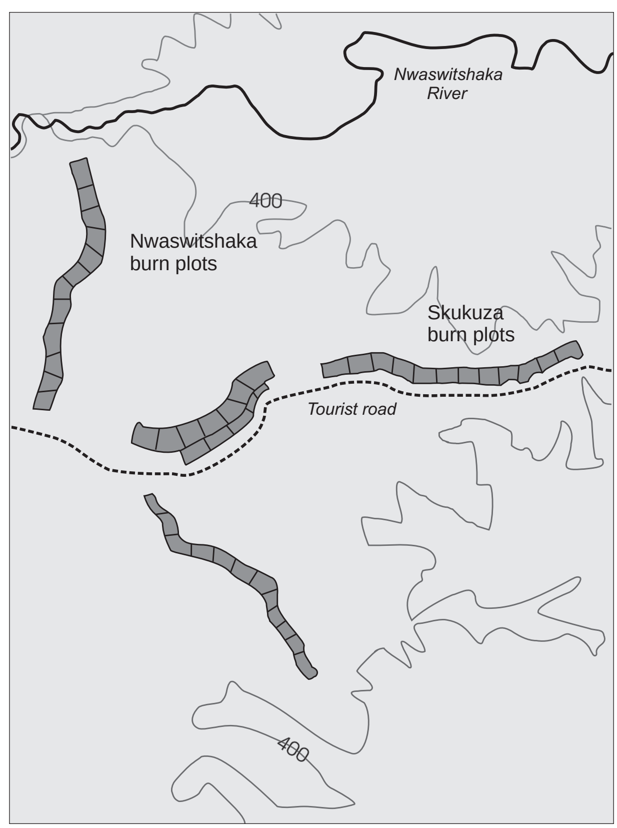

FIG. 1 Configuration of the experimental burn plot replicates located north and south of the road between the tourist rest camps of Skukuza and Pretoriuskop. The sub-plots in the westerly replicate are referred to as the Nwaswitshaka burn plots and those in the easterly replicate as the Skukuza burn plots

mental burning regimen required that all five sub-plots at both localities were burned in 2000, three during August and two during October.

Ticks were collected at approximately monthly intervals from January 1999 to March 2002 by drag-sampling the vegetation of the selected sub-plots. This was done by an operator dragging a wooden spar, with 10 x 10 cm x 100 cm weighted flannel strips attached to it, for 200 m over the vegetation of each sub-plot. After each drag all instars of all ticks on the flannel strips were collected by means of forceps and stored in 70 % ethanol in labelled glass vials. At every occasion the drags were repeated six times at approximately 50 m intervals in each sub-plot, and a total of 42 x 200 m long drags were thus made within each of the two experimental burn plot replicates and their outside control localities every month. With few exceptions sampling was performed during the third week of each month so that it did not coincide with the experimental burning.

There were no drags during February 1999 because of rain, and none in February and March 2000 because of flooding in the southern regions of the park following more than 400 mm rain during February (Fig. 2). Rain during September 2000 again prevented sampling, while one of the sub-plots and both outside control areas could not be sampled during September 2001 because they were still smouldering after a huge accidental fire in the south-east of the park had jumped the fire-breaks surrounding the burn plots.

Data analysis

The tick counts were $\log_{10}$ transformed prior to analysis to reduce the effects of overdispersion (Petney, Van Ark & Spickett 1990). The seasonality of each species and stage was then tested for both locations using autocorrelation (SPSS Inc. 1994). *Amblyomma marmoreum*, *Rhipicephalus appendiculatus* and *Rhipicephalus zambeziensis* exhibited a pronounced periodicity with peaks from the summer to early winter and a marked decline in numbers in the late winter and early spring. The analyses for these species were restricted to the period from January to July, the months with the highest numbers. This reduced the number of drags with zero counts, and because burning occurred in the late winter or early spring, collections from the preceding burn year were eliminated.

To analyse the effect of burning, the year after burning was classed as the first, second or third, or unburned (control). However, the decline in tick numbers in 2001 following the burning of both sets of five sub-plots in 2000 was also confounded by the marked decrease in rainfall from 1999/2000 to 2000/2001 (Fig. 2). To allow for temporal variation among calendar and climatic years, a second variable was created with four periods corresponding to the calendar year after burning: Period 1 [prior to burn month (August or October) in 1999], Period 2 (from burn month in 1999 to burn month in 2000), Period 3 (from burn month in 2000 to burn month in 2001), and Period 4 (October 2001 to March 2002). The total tick data and data for each species were then analysed using a three factor analysis of variance with location, period and year after burning. Because year after burning was not balanced across periods, and there were often significant period effects, a multiple classification analysis (SPSS Inc. 1994) was used to adjust the means for the effect of the other variables.

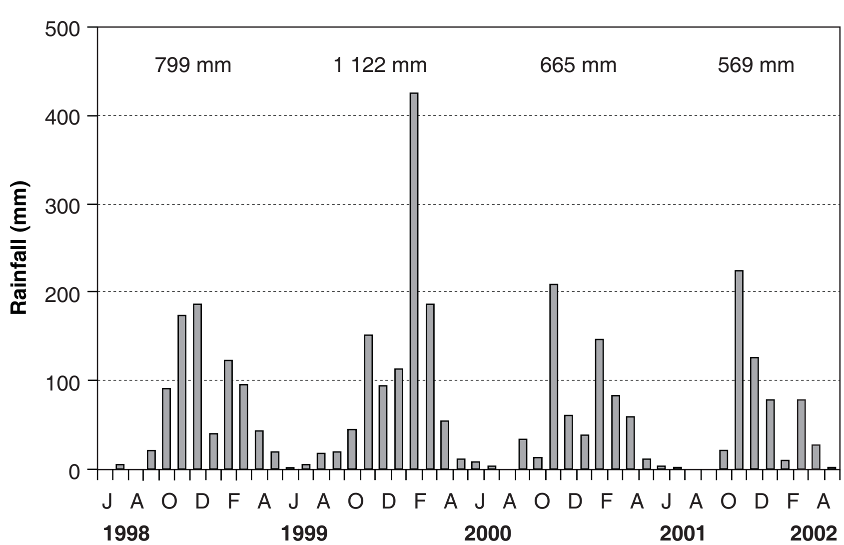

FIG. 2 Monthly rainfall (mm) measured at the Skukuza tourist rest camp during the collection period. The numbers in the figure represent total annual rainfall (June to May)

RESULTS

Fourteen tick species were collected (Table 1). *Amblyomma hebraeum* and *Rhipicephalus (Boophilus) decoloratus* were the most common species at both sites. *Amblyomma marmoreum*, *Haemaphysalis leachi*, *R. appendiculatus*, *Rhipicephalus evertsi evertsi*, *Rhipicephalus simus* and *R. zambeziensis* were also commonly collected. With the exception of *H. leachi* and *R. simus*, whose adults were most routinely recovered, larvae were the most frequently collected stage.

Total ticks

More ticks were collected from the Nwaswitshaka burn plots than from the Skukuza burn plots ($P \leq 0.001$). There was no evidence of seasonality at either location. There was a significant difference among periods ($P = 0.002$) with lower numbers in

TABLE 1 Total numbers (proportions %) of ticks collected from two sets of experimental burn plots in the Kruger National Park, South Africa

Tick species	Stage of development	Locality: Skukuza		Locality: Nwaswitshaka	
Amblyomma hebraeum	LL	39 980	(84.21)	35 704	(65.66)
	NN	25	(0.05)	23	(0.04)
	AA	1		0	
Amblyomma marmoreum	LL	102	(0.21)	1 690	(3.11)
	NN	1		2	
Rhipicephalus (Boophilus) decoloratus	LL	3 928	(8.27)	10 895	(20.04)
	AA	1		0	
Dermacentor rhinocerinus	LL	5	(0.01)	24	(0.04)
Haemaphysalis leachi	LL	2		5	(0.01)
	NN	3	(0.01)	4	(0.01)
	AA	921	(1.94)	960	(1.77)
Haemaphysalis spinulosa	AA	0		1	
Haemaphysalis zumpti	AA	0		2	
Hyalomma truncatum	LL	1		1	
	AA	0		1	
Rhipicephalus appendiculatus	LL	418	(0.88)	939	(1.73)
	NN	10	(0.02)	56	(0.10)
	AA	5	(0.01)	6	(0.01)
Rhipicephalus evertsi evertsi	LL	535	(1.13)	1 816	(3.34)
	AA	0		1	
Rhipicephalus follis	AA	1		0	
Rhipicephalus simus	LL	12	(0.03)	14	(0.03)
	NN	2		1	
	AA	455	(0.96)	340	(0.63)
Rhipicephalus turanicus	AA	0		1	
Rhipicephalus zambeziensis	LL	1 023	(2.15)	1 847	(3.40)
	NN	37	(0.08)	39	(0.07)
	AA	9	(0.02)	3	(0.01)
Total		**47 477**	**(100.00)**	**54 375**	**(100.00)**

LL = Larvae
NN = Nymphs
AA = Adults

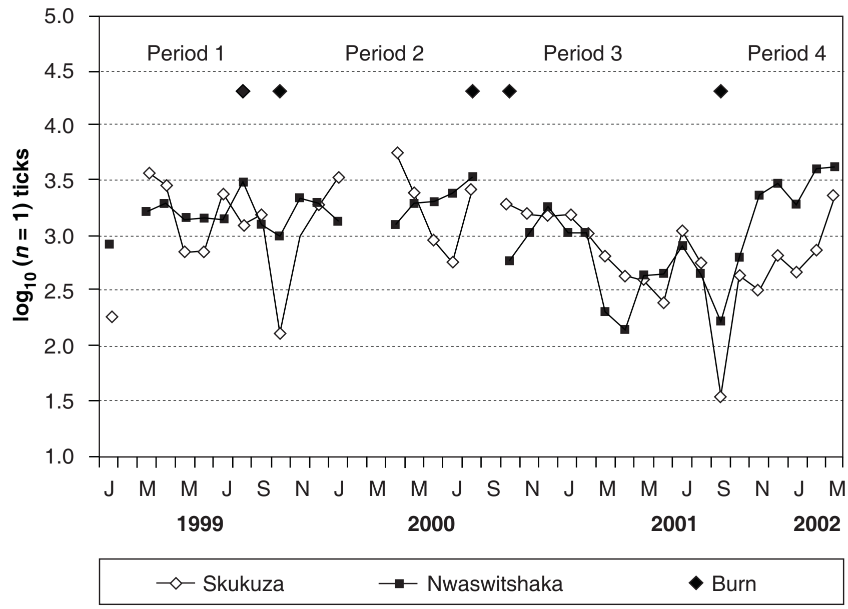

FIG. 3 Total number of ticks collected each month from the vegetation of all plots combined at Skukuza and at Nwaswitshaka. Period 1 [prior to burn month (August or October) in 1999]; Period 2 (from burn month in 1999 to burn month in 2000); Period 3 (from burn month in 2000 to burn month in 2001); and Period 4 (October 2001 to March 2002). ◆ indicates month of burning

Period 3 (2000/2001) than in the other periods (Fig. 3). Comparing between years after burning, the second year after burning and the unburned sub-plots had significantly higher tick numbers than the first and third years after burning (Table 2). Burning *per se* appeared to have little effect on the number of ticks collected, as there was no consistent pattern in the number of ticks recovered 1–2 weeks after a burn and the number recovered in the preceding month or in the subsequent 1–2 months. In 2000/2001 there was a marked drop in tick numbers relative to the preceding years in the burned sub-plots, but little change from the other years in the unburned sub-plots.

Amblyomma hebraeum

Amblyomma hebraeum larvae were the most commonly collected ticks, accounting for 84.2 % of those collected at Skukuza and 65.7 % of those at Nwaswitshaka. The numbers did not differ significantly between the two locations ($P > 0.15$), and there was no evidence of seasonality. There was a significant difference among periods ($P = 0.01$) with Periods 2 (1999/2000) and 4 (2001/2002) having higher numbers than Periods 1 (1999) and 3 (2000/2001) (Fig. 4A). There was also a significant difference among years after burning ($P = 0.001$) with the second year after burning and unburned sub-plots having higher numbers than the first and third years after burning (Table 2). The difference among years after burning was more pronounced at Nwaswitshaka than at Skukuza. At Nwaswitshaka the decrease in the numbers of *A. hebraeum* larvae in Period 3 occurred on both the unburned and burned sub-plots suggesting that it was related to the drier conditions in 2000/2001, but there was no effect at Skukuza. Burning *per se* appeared to have little effect on the number of *A. hebraeum* larvae recovered, as there was no consistent pattern in the number collected 1–2 weeks after a burn and the number collected in the preceding month or in the subsequent 1–2 months.

Amblyomma marmoreum

Amblyomma marmoreum larvae were collected from January to October (Fig. 4B), with the highest numbers from March to August. They were most common at Nwaswitshaka ($P < 0.001$). The numbers were highest in 2000, and none were collected in 2002 ($P < 0.001$). There was no significant difference ($P = 0.12$) among the years after burning.

Rhipicephalus (Boophilus) decoloratus

Rhipicephalus (Boophilus) decoloratus larvae were the second most commonly collected tick (Table 1). The numbers were significantly higher ($P < 0.001$) at Nwaswitshaka, where they accounted for 20.0 % of the ticks collected, than at Skukuza where they accounted for 8.3 % of the ticks collected. There was no evidence of seasonality. The numbers were significantly lower in Period 3 than in the other periods ($P < 0.001$), and significantly lower in Period 4 than in Period 2 ($P < 0.05$) (Fig. 4C). The numbers were higher in the second year after burning than in the first and third years and in the unburned sub-plots ($P = 0.009$). Burning *per se* did not appear to affect the numbers of *R. (B.) decoloratus* larvae.

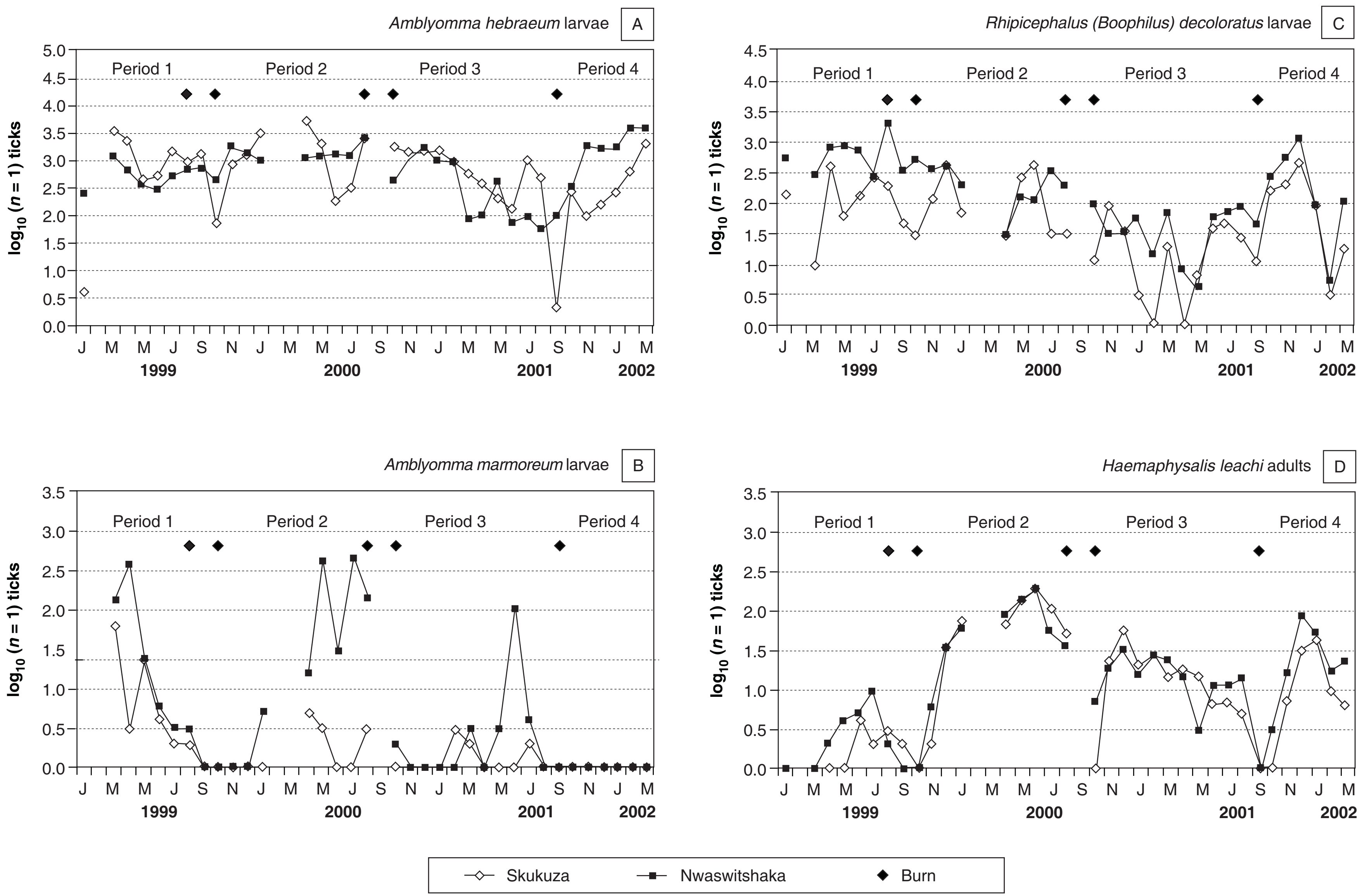

FIG. 4 Total number of (A) *Amblyomma hebraeum* larvae, (B) *Amblyomma marmoreum* larvae, (C) *Rhipicephalus (Boophilus) decoloratus* larvae, and (D) *Haemaphysalis leachi* adults collected each month from the vegetation of all plots combined at Skukuza and at Nwaswitshaka. Period 1 [prior to burn month (August or October) in 1999]; Period 2 (from burn month in 1999 to burn month in 2000); Period 3 (from burn month in 2000 to burn month in 2001); and Period 4 (October 2001 to March 2002). ◆ indicates month of burning

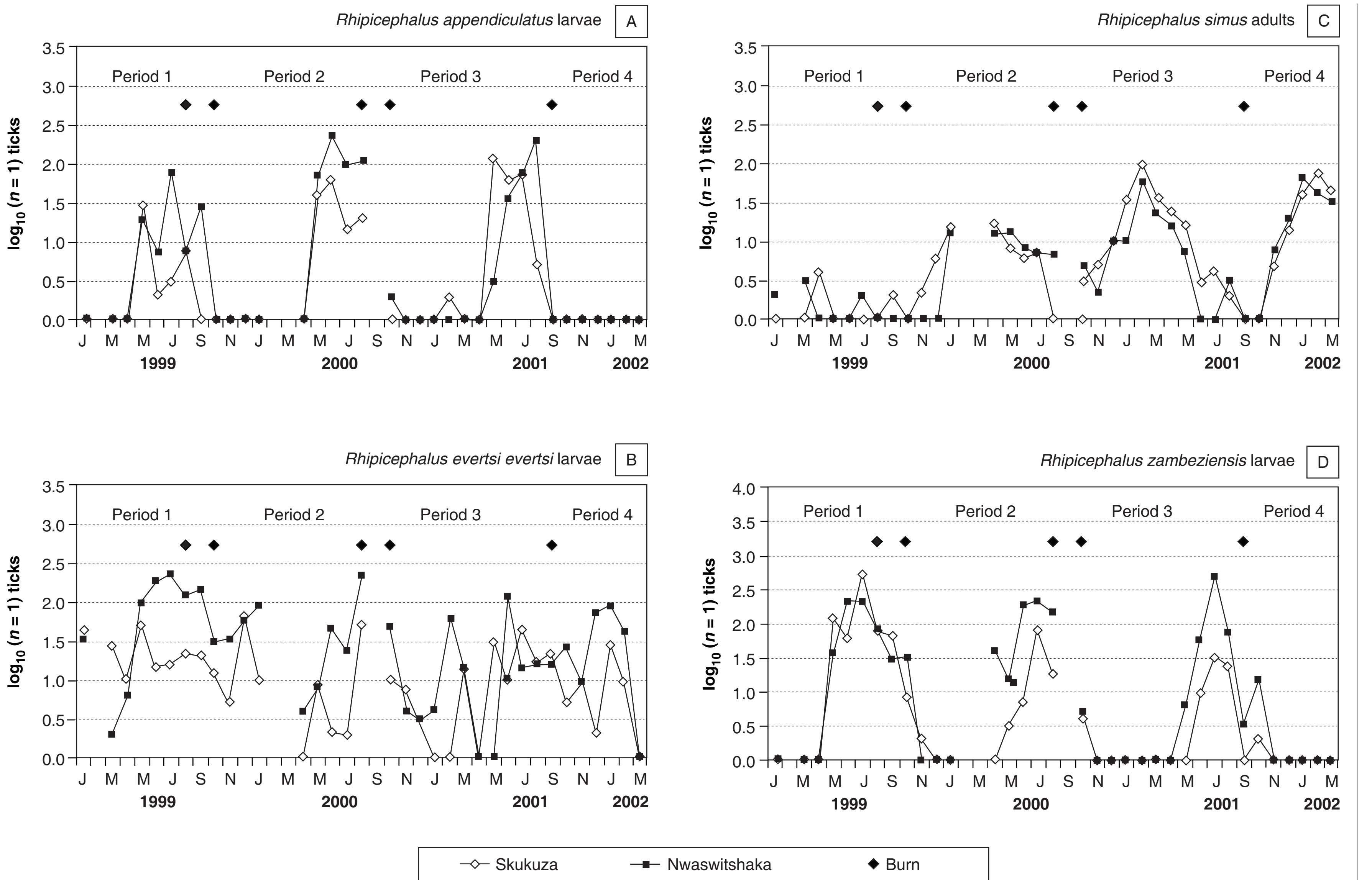

FIG. 5 Total number of (A) *Rhipicephalus appendiculatus* larvae, (B) *Rhipicephalus evertsi evertsi* larvae, (C) *Rhipicephalus simus* adults, and (D) *Rhipicephalus zambeziensis* larvae collected each month from the vegetation of all plots combined at Skukuza and at Nwaswitshaka. Period 1 [prior to burn month (August or October) in 1999]; Period 2 (from burn month in 1999 to burn month in 2000); Period 3 (from burn month in 2000 to burn month in 2001); and Period 4 (October 2001 to March 2002). ◆ indicates month of burning

TABLE 2 Adjusted means ($\log_{10}$ transformed) for the number of ticks collected each month in the burn plots by year after burning. Values with the same superscript are not significantly different ($P > 0.05$)

Tick species and stage of development	Year after burning			
	1	2	3	Unburned
Total ticks	1.81[a]	2.12[b]	1.86[a]	2.10[b]
Amblyomma hebraeum larvae	1.47[a]	1.71[b]	1.28[a]	1.74[b]
Amblyomma marmoreum larvae (January to July)	0.15[a]	0.16[a]	0.01[a]	0.19[a]
Rhipicephalus (Boophilus) decoloratus larvae	0.75[a]	1.02	0.75[a]	0.86[a]
Haemaphysalis leachi adults (December 1999 to March 2002)	0.37	0.75[a]	0.77[a]	0.65[a]
Rhipicephalus appendiculatus larvae (May to July)	0.67[a]	0.32[b,c]	0.12[c]	0.48[a,b]
Rhipicephalus evertsi evertsi larvae	0.40[a]	0.36[a]	0.40[a]	0.21
Rhipicephalus simus adults	0.15	0.24[a]	0.30[a]	0.33[a]
Rhipicephalus zambeziensis larvae (May to July)	0.75[a]	0.67[a]	0.45[a]	0.90[a]

Haemaphysalis leachi

Most of the *H. leachi* collected were adults (Table 1). The numbers did not differ between the two locations ($P > 0.5$), and there was no evidence of seasonality. The numbers of *H. leachi* adults changed markedly over time ($P < 0.001$), with few in the first year, an increase over the next 6 months, then a decrease to August 2001 and reappearance in November 2001 (Fig. 4D). The numbers were lower the first year after burning than in the other years ($P < 0.001$). The effect of burning *per se* was difficult to determine because adult tick numbers usually decline on the vegetation in the park during the late winter (Horak, Emslie & Spickett 2001).

Rhipicephalus appendiculatus

Rhipicephalus appendiculatus exhibited a pronounced seasonal periodicity. Larvae were present from February to October with peak occurrence from May to August, nymphs were present from June to February with a peak in August to October, and the adults were collected from February to April (Fig. 5A). *Rhipicephalus appendiculatus* larvae and nymphs were most common at Nwaswitshaka ($P = 0.035$ and $P < 0.001$, respectively). There was a marked increase in number of larvae from 1999 to 2000 in both areas and a decline in 2001 ($P < 0.001$). The number of nymphs also appeared to increase from 1999/2000 to 2000/2001, but did not appear to decline in 2001/2002. The numbers of larvae were higher in the first year after burning and lowest in the third year after burning ($P = 0.004$). The immediate effect of burning on larvae could not be assessed because the seasonal decline in numbers coincided with the timing of the fires. Nymphs were collected 1–2 weeks after burning, but the numbers were too low to assess the immediate impact of the fire.

Rhipicephalus evertsi evertsi

Rhipicephalus evertsi evertsi larvae were present throughout the year, with no evidence of seasonality (Fig. 5B). They were more common at Nwaswitshaka than at Skukuza ($P < 0.001$). There was a significant difference among periods ($P < 0.001$) as the numbers declined from Period 1 to Period 3, then increased in Period 4. The numbers were significantly higher on the burned sub-plots than on the unburned sub-plots ($P = 0.004$).

Rhipicephalus simus

Most of the *R. simus* collected were adults (Table 1). They were more common at Skukuza than at Nwaswitshaka ($P = 0.028$). The numbers increased from 1999 to 2001/2002, and there was a marked seasonality with the highest numbers from January to March and the lowest numbers from August to October (Fig. 5C). The numbers increased with year after burning ($P < 0.001$).

Rhipicephalus zambeziensis

Rhipicephalus zambeziensis was more common than *R. appendiculatus* in both areas. There was a pronounced seasonality for all stages (Fig. 5D). Larvae were collected from April to November with a peak in July, nymphs were collected from May to January with a peak in August, and adults were collected from February to April. *Rhipicephalus zambeziensis* larvae were more common at Nwaswitshaka than at Skukuza ($P = 0.001$), but the number of nymphs did not differ between the two areas. The numbers of larvae decreased from the first to the third year after burning, but the change was not statistically significant ($P = 0.16$). The immediate effect of burning on larvae could not be assessed because the seasonal decline in numbers coincided with the timing of the fires. As with *R. appendiculatus*, *R. zambeziensis* nymphs were collected on burned sub-plots 1–2 weeks after burning, but the numbers were too low to determine the immediate impact of the burn.

DISCUSSION

Dragging is only effective for sampling those ticks and developmental stages that quest for hosts from the vegetation and that are inclined also to attach to flannel strips. Hence dragging may limit the tick species and life stage spectrum of any investigation that relies on it as the only sampling method.

Amongst the 14 tick species collected from the burn-plots the larvae of *A. hebraeum*, *A. marmoreum*. *R. (B.) decoloratus*, *R. appendiculatus*, *R. e. evertsi* and *R. zambeziensis* quest from vegetation and are inclined to attach to flannel. Although the nymphs and adults of *R. appendiculatus* and *R. zambeziensis* also quest from vegetation, they are less inclined to attach to flannel than the larvae. On the other hand, the adults of *H. leachi*, that prefer carnivores as hosts (Horak, Braack, Fourie & Walker 2000a), and of *R. simus*, that prefer monogastric animals such as carnivores, equids and suids as hosts (Walker, Keirans & Horak 2000), also quest from the vegetation and readily attach to flannel. They are probably enticed to do so by chemicals exuded by the omnivorous, monogastric persons dragging the flannel strips, and they are also amongst the tick species that are most frequently recorded as attaching to humans (Horak, Fourie, Heyne, Walker & Needham 2002). The adults of the rhinoceros tick *D. rhinocerinus* also quest from vegetation, but prefer grass species with long, thick stems, which, although present, are sparse on the burn-plots. The nymphs and adults of *A. hebraeum* and *A. marmoreum*, the larvae and nymphs of *D. rhinocerinus*, *H. leachi* and *R. simus*, the larvae and adults of *H. truncatum* and the adults of *R. e. evertsi* (the latter two ticks both have two-host life cycles) all quest for hosts from the soil surface or its immediate vicinity and are seldom collected by dragging.

With the exception of *H. truncatum*, all the major tick species that occur in the park were collected from the experimental burn-plots in sufficient numbers to make analysis possible. Without any doubt *H. truncatum* was also present on the plots as adults and larvae on the soil surface and as adults on large animals such as giraffes and zebras and as larvae and nymphs on scrub hares and gerbils (Horak, Potgieter, Walker, De Vos & Boomker 1983; Horak, De Vos & De Klerk 1984; Horak, Spickett, Braack & Penzhorn 1993; Horak 1998; Braack, Horak, Jordaan, Segerman & Louw 1996). In our experience, however, very few, if any, *H. truncatum* can be collected by drag-sampling and consequently its favoured host animals have to be examined in order to determine its presence at a particular locality.

The effects of burning on tick populations are complex because fires may affect both ticks and their host species (Spickett *et al*. 1992). Fires alter the physical environment and the nature and quatity of food and cover available to animals (Bigalke & Willan 1984). Questing ticks may be destroyed in a fire (Bigalke & Willan 1984), but some species may also exhibit avoidance strategies that enhance survival (Frost 1984). The direct impact on other free-living stages, and on small mammal hosts, will depend on the intensity of the burn. Increased temperatures and a decrease in soil moisture on burned areas (Cass, Savage & Wallis 1984) may increase the mortality of free-living ticks, although the increased temperatures may also accelerate temperature-dependent development (Spickett *et al*. 1992). Burning may also affect tick populations by altering the spatial distribution of preferred and other hosts. Many herbivores select the new growth in the burned areas (Gureja & Owen-Smith 2002; Tomor & Owen-Smith 2002; Wronski 2003; Zavala & Holdo 2005), but the populations of small mammals and birds requiring ground cover may decline (Frost 1984).

All stages of development of *A. hebraeum*, the most commonly collected species at both locations, can be found on large herbivorous animals, the size of kudu bulls and larger, as well as on warthogs (Horak, MacIvor, Petney & De Vos 1987; Horak, Boomker, De Vos & Potgieter 1988; Horak, Boomker, Spickett & De Vos 1992). With the exception of rodents, on which they do not occur, the nymphs and particularly the larvae can be found on most smaller animals, including antelopes, zebras, large and small carnivores, hares, guineafowls and leopard tortoises (Horak *et al*. 1984; 1993; 2000a; Horak, Spickett, Braack & Williams 1991; Braack *et al*. 1996; Horak 1998). This, coupled with the fact that all stages of development are present throughout the year in the park (Horak *et al*. 1992), and that the females lay exceptionally large numbers of eggs (Norval 1974), ensure that the larvae of *A. hebraeum* are more numerous on the vegetation in most habitats in the park than those of other ticks (Spickett, Horak, Braack & Van Ark 1991). Fire did not appear to have an immediate effect on the numbers of questing larvae, suggesting that many survived the fire. While there were statistically significant differences among the years after burning, there was not a consistent trend, indicating that fire has no long-term effect probably because engorged female *A. hebraeum* are continuously brought on to the burn plots by their various large herbivorous hosts.

All stages of development of *A. marmoreum* prefer leopard tortoises (Horak, McKay, Heyne & Spickett 2006). Fire may kill many tortoises because of their limited ability to escape (Branch 1998), but larger bird species such as helmeted guineafowls and pheasants, as well as carnivores, large herbivores and scrub hares can harbour considerable numbers of larvae and some nymphs of this tick (Horak *et al*. 1991; 1993; 2000a; 2006; Uys & Horak 2005). Burning did not have a significant effect on the numbers of questing *A. marmoreum* larvae. There was a seasonal decline in the number of larvae at the time of the burns, and the 4–6 month delay between the burns and reappearance of questing larvae was probably adequate for re-colonization of the burned plots by the preferred hosts.

The one-host tick, *R. (B.) decoloratus* infests especially kudus, bushbuck, impalas and zebras in the park (Horak *et al.* 1983; 1984; 1992; Horak, Gallivan, Braack, Boomker & De Vos 2003). It is present throughout the year, but is most numerous on its hosts during spring and mid-summer, and probably completes two if not three life cycles annually. Consequently animals browsing or grazing on the burn plots, or just walking through shortly after the spring burns, will carry in large numbers of engorged female ticks. The interval between the detachment of these females and the hatching of larvae from the eggs they have laid can be as short 40 days during the summer (Spickett & Heyne 1990). Burning did not appear to have an immediate effect on the number of larvae, suggesting that substantial numbers survived the fire, or that the changes in microclimate after the burn accelerated development (Spickett *et al*. 1992). The increase in numbers in the second year after the burn may be the consequence of increased use of the burned area by preferred hosts the first year after burning.

The occurrence of two other major tick species, namely *R. appendiculatus* and *R. zambeziensis* in nearly equal numbers on the burn-plots is fortuitous. Both ticks are present in the park, but often separately in habitats only a few km apart (Horak 1998). Judging by the small numbers collected from the burn plots these were not located in an ideal habitat for either species and probably lie in a transitional zone. Minshull & Norval (1982) recorded an increase in the number of *R. appendiculatus* larvae collected the year after burning in *Hyperrhaenia* grassland on clay, but not on sandy soil. This is consistent with increases in *R. appendiculatus* and *R. zambeziensis* larvae the year after burning in the present study. This is probably caused by the influx of "burn grazers" after the fire.

The larvae and nymphs of *D. rhinocerinus*, *H. leachi*, *R. simus* and *R. turanicus* use small rodents as hosts (Norval 1984; Walker *et al*. 2000; Horak & Cohen 2001; Petney, Horak, Howell & Meyer 2004), as do the larvae of *H. truncatum* (Braack *et al*. 1996). While many small mammals survive fire, there are often marked declines in the populations of some species after a burn because of the habitat changes (Frost 1984). A reduction in the population of the hosts of their immature stages would explain the significant reduction in the numbers of adult *H. leachi* and *R. simus* collected the first year after the burn. A pack of wild dogs, with a den in the vicinity of the plots, probably played a role in seeding the area with engorged female *H. leachi* and particularly *R. simus* (Norval 1984; Horak *et al*. 2000a).

The immature stages and adults of *R. e. evertsi* utilize zebras as hosts, and can be found on these animals throughout the year (Horak *et al.* 1984). Gureja & Owen-Smith (2002) and Tomor & Owen-Smith (2002) list zebras as one of the species preferentially using burnt areas. These animals were often seen on the plots, both before and after burns, and probably seeded them with engorged nymphs and females as well as with the females of *R. simus*, which also feed on them.

Surveys on the seasonality of ticks on eight host species, ranging in size from gerbils to kudus, and including helmeted guineafowls, as well as on the vegetation of two landscape zones in the park, have been conducted intermittently since 1978 (Horak 1998). These have shown that the only stages of development present on the vegetation in substantial numbers at the time of the burns in August or October are larvae of *R. (B.) decoloratus* and nymphs of *R. appendiculatus* and *R. zambeziensis*. Thus, a burn in August or October is only likely to have a direct effect on peak numbers of single life stages of the abovementioned three major tick species. The larvae of *A. hebraeum* and *R. e. evertsi* may also be present at this time, but are non-seasonal without defined peaks in numbers. Depending on the heat generated by the fire, various life stages of other ticks questing for hosts on the soil surface, or moulting or ovipositing in sheltered spots, may also be adversely affected.

One of the reasons for the apparent lack of effect of fire on the numbers of ticks questing for hosts from the vegetation in the present investigation could be the small size of the individual sub-plots. Although 7 ha may seem large, in the context of a large wildlife reserve and free access by animals, the plots should probably have been 10 times larger. The apparent ease with which the 7 ha sub-plots can be re-colonised by small mammals or accessed by large animals either for foraging, loafing or simply as walkways, add innumerable variables to the already complex analysis of the effects of fire on questing ticks.

Finally, the free-living stages of ticks of sub-Saharan Africa have been exposed to intermittent fires for millions of years and have probably been selected for survival strategies as yet unknown to us. Consequently they have, and probably will, successfully survive the effects of fire for centuries to come.

CONCLUSION

Unless animals are excluded from recently burned localities the effects of fire on free-living tick numbers are likely to be minimal and of short duration.

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