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Managing grassland for wildlife: the effects of rotational burning on tick presence and abundance in African savannah habitat

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Ticks are obligate blood-feeding ectoparasites that have negative effects on animals through blood loss and vectoring disease. Controlling ticks is a major aspect of wildlife management in many areas, including African savannah where ticks are a long-standing problem. Rotational burning of vegetation is widely thought to reduce ticks but empirical data are lacking. We investigate the effect of block rotational burning on tick populations in a South African wildlife reserve. We measured tick presence/abundance using tick drags in multiple blocks of five different burn ages (areas burned 1, 2, 3, 4 or 5 years previously). We also assessed herbivore diversity using dung as a proxy. Tick presence was highest in areas burned 2–3 years previously. It was lowest in recently-burned areas (probably due to fire-induced mortality or loss of field-layer refugia) and areas burned ≥ 4 years previously (probably because the lack of palatable grass meant herbivore abundance was lower; this is supported by significantly lower herbivore presence in old burns and significant positive correlation between tick numbers and herbivore presence). Burn age and, to a lesser extent, block, were significantly related to tick presence and abundance at both larval and nymph stages. The model that best explained tick numbers, though, included the interaction between burn age and block due to substantial inter-block variability in mid-burn blocks relative to lower variability in blocks at the start or end of the burn cycle. This suggests that burn age and block-specific conditions together influence tick abundance, with habitat heterogeneity likely being an important modifier of the effect burning has on tick numbers. Although annual burning of large areas would not be feasible while maintaining suitable grazing, we suggest that additional annual burning of potential wildlife (and therefore tick) hotspots, such as around waterholes, could reduce tick populations and improve wildlife management.

At least 867 species of hard-bodied tick (Acari; Ixodidae) have been classified worldwide. As obligate blood-feeding ectoparasites, many species have a significant negative effect on their hosts, with direct effects including exsanguination and anaemia (Walker et al. 2003, Latif and Walker 2004, Pfitzer et al. 2011). Indirect effects are often more serious as ticks can vector pathogenic bacteria (e.g. *Borrelia* and *Rickettsia*), protozoa (e.g. *Babesia* and *Cytauxzoon*), and viruses (e.g. those causing tick-borne meningoencephalitis and some haemorrhagic fevers) (Sonenshine 1991, Bryson et al. 2000, Walker et al. 2003, Steyl et al. 2012, Brown et al. 2013, del Fabbro et al. 2015). Bite wounds can also be susceptible to secondary infection. As well as posing a severe risk to human health (del Fabbro et al. 2015), ticks can have substantial

impacts on animals. Farmers often use acaricides to protect livestock (Latif and Walker 2004, Jongejan and Uilenberg 2004, Kivaria 2006), either by direct application or, in the case of large-scale game farms, using automated acaricide dispensers. For National Parks and other wildlife reserves, though, acaricide treatment is expensive and unlikely to be a practical solution (Moyo and Masika 2009). Managers of wildlife in such areas must thus use alternative methods to control tick numbers and protect animals from tick bites and tick-borne diseases.

Globally, one of the most common non-acaricide methods for controlling tick populations is burning (West 1965, Gleim et al. 2014). As burning can be applied at a landscape scale reasonably quickly and cost efficiently, several studies have investigated the efficacy of this as a control method (Drew et al. 1985, Spickett et al. 1992, Stafford et al. 1998, Fyumagwa et al. 2007). However, data are conflicting and there are substantial differences in the reported efficacy of this method. Such variation is likely to be partly due to studies being undertaken in different ecosystems on different species

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(Spickett et al. 1992), but may also stem from realistic operational management scenarios not being accurately reflected in small-scale experimental research plots (Horak et al. 2006, Gleim et al. 2014).

Most studies on the effects of burning on tick abundance agree that there is an immediate decline in ticks following fire (Hoch et al. 1972, Cully 1999, Fyumagwa et al. 2007, Allan 2009, Adams et al. 2013). This could be caused by direct mortality when temperatures exceed 150–165°C for at least 15 s (Scrifes et al. 1988) or because tick refugia within the field layer are reduced or eliminated (Polito et al. 2013). There are exceptions though; Padgett et al. (2009) showed that burning had no effect on tick numbers in Californian chaparral for species that were able to utilise soil refugia to escape fires; this might also be the case for species that typically quest on soil rather than vegetation (Bryson et al. 2000). The long-term effects of burning on tick numbers are even less clear (Spickett et al. 1992). For example, one study has found that post-burn ecological conditions maintain tick numbers at a low level for at least three years (Fyumagwa et al. 2007), while several studies have concluded that tick numbers recover to pre-burn levels (or sometimes even higher) within one or two years post-burn (Scrifes et al. 1988, Allan 2009, Adams et al. 2013).

In many areas of southern Africa, grassland within wildlife reserves, conservation areas and national parks is managed through burning. This is typically undertaken to optimise available grazing by removing dominant rank grasses thereby allowing new growth of more palatable species (Hardy et al. 1999). Such burning is often undertaken rotationally in blocks every few years to ensure that there is always sufficient palatable grass for herbivores. This creates heterogeneity in space and time that is sometimes termed mosaic patch pyrodiversity (Parr and Brockett 1999, Parr and Andersen 2006). Rotational burning also has the effect of moving animals around sites thereby avoiding localised overgrazing. Generally, the need to manage grassland for biodiversity is what drives rotational burning within bushveld ecosystems (Martin and Sapsis 1992). It is sometimes considered to have additional benefit in controlling tick numbers but empirical evidence for this is lacking (Spickett et al. 1992). Establishing an evidence base for rotational burning as a tick management strategy is also likely to be complicated by the fact that fire causes landscape-scale relocation of animals – the tick hosts.

The need to investigate the effects of prescribed burning on tick numbers has been highlighted as a research priority (Wilkinson 1979, Gleim et al. 2014). This is especially true for rotational management in African savannah grassland ecosystems, which are some of the most biodiverse areas on the planet particularly for mammals (Groombridge 1992, Wynberg 2002), where ticks are a numerous, widespread and long-standing problem (Moore 1912, Horak et al. 2006, Brown et al. 2013), and where the effects of fire are much less clear than is often believed (Parr and Anderson 2006). In this study, we aim to establish the effect of burn history on tick presence and abundance using a large and long-established rotational burn management system in a South African wildlife reserve to establish the most effective inter-burn period for tick control. We also relate tick numbers

to herbivore presence using dung as a proxy. We test two opposing hypotheses: 1) that the lowest tick numbers will be in the most recently burned areas and 2) that the lowest tick numbers will be in the areas burned a long time previously.

Methods and material

Study site

This study was carried out in autumn (April–May) 2015 at Mankwe Wildlife Reserve located in Northwest Province, South Africa. During the study period, the weather was dry with a mean diurnal maximum temperature of 28–32°C and a mean nocturnal minimum temperature of 8–10°C. The site is managed as a wildlife reserve and supports about 1500 large mammals including impala *Aepyceros melampus*, blue wildebeest *Connochaetes taurinus*, greater kudu *Tragelaphus strepsiceros*, common eland *Taurotragus oryx*, zebra *Equus quagga* and giraffe *Giraffa camelopardalis*. Animals can roam freely across the reserve and populations are managed as necessary. No direct (acaricide) tick management is currently undertaken.

Sampling strategy

The reserve covers an area of 47 km² and is surrounded by an electrified 18-wire game-proof perimeter fence. Immediately inside the fence is an unmanaged boundary buffer strip of tall grass and some scrub to decrease visibility into the reserve and poaching risk; this is ~80–100 m in width. The interior is divided into 16 blocks of unequal size (min = 0.6 km²; max = 4 km²; mean = 1.8 km²; SD = 1.4 km²). These are separated by firebreaks, which are typically ~100 m wide. The blocks are burned on a rotational basis, with each block having been burned once every four to five years for the last 25 years. Burning is undertaken during the winter (dry season).

At the time of our 2015 study, there were three blocks that had been burned five years previously (2010; total = 2.1 km²), three blocks burned four years previously (2011; total = 4.1 km²), three blocks burned three years previously (2012; total = 6.6 km²), four blocks burned two years previously (2013; total = 9.4 km²), and three blocks that had been burned the previous year (2014; total = 6.4 km²) (n = 16 blocks summing to 18.3 km²). Within each of these 16 blocks, three points were selected using random co-ordinates. The parts of the reserve outside of the block burn areas (e.g. boundary buffer strip, firebreaks, waterbodies) were excluded. The grassland habitat of the site can be seen in Fig. 1. Vegetation characteristics of each burn age are described in Table 1; sward height was determined using the direct measurement method described in Stewart et al. (2001) and species composition was based on veld condition assessments (Hardy et al. 1999), which is undertaken regularly at the reserve to monitor the effectiveness of burning on grass composition and nutritional value. There are water bodies (dams or artificial pans) within or adjacent to all blocks to allow animals to disperse across the entire reserve rather than aggregating solely in areas with water.

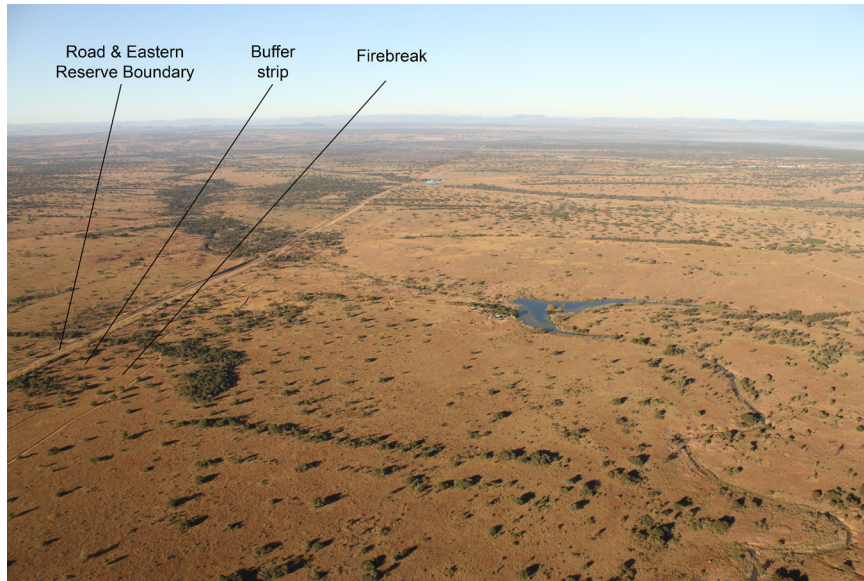


Figure 1. Aerial view of the grassland habitat of the study site. The road marks the eastern boundary of the reserve, inside of which are the buffer strip and then the firebreak as described in the Methods.

Tick surveying

Ticks were sampled using a white tick drag made from durable flannel material backed with a plastic coating. The drag was 1.2 m² and the central 1m² was marked with a 10 × 10 grid using permanent marker; this was the sampling zone and only ticks within this area were counted. At each survey point, ten 20 m tick drags were carried out radially from the centre point at a slow walking speed with the flannel material dragged so it was in contact with the grass to collect ticks (more details in Spickett et al. 1992). Tick surveying was conducted between 08:30 a.m. and 17:00 p.m. In recognition of the fact that tick activity might have a diurnal pattern, a systematic sampling strategy was adopted so that of the three points in each of the 16 blocks, one was surveyed during the early part of the day (08:30–10:30), one was surveyed during the middle part of the day (11:00–14:30) and one was surveyed during the late part of the day (15:00–17:00). In total, 9600 m² of grassland was surveyed across 480 tick drag transects (200 m² per survey point × 3 survey points per block × 16 blocks across the 5 different burn ages). At the end of each drag, the ticks collected were

counted within each life stage by the same two researchers (co-authors ANH and RLK). Larvae were differentiated from nymphs based on the number of legs (six versus eight, respectively). The drag was brushed thoroughly to ensure that all ticks were removed before carrying out the next drag. All ticks were identified as Ixodidae (hard ticks) based on: 1) mouthparts projecting anteriorly and thus being visible with the specimen held in dorsal view; and 2) the presence of a scutum, a tough sclerotised plate on the dorsal body surface, limited to the anterior ~1/3 of the dorsal region in both larvae and nymphs (Walker et al. 2003, Madder et al. 2015). Ticks were not identified to genus/species as they were exclusively immature stages (primarily larvae) when morphological identification for southern African species relies upon comparing mouthparts to co-occurring adults in the field (Walker et al. 2003).

Dung surveying

Following behind the tick drag was an experienced local tracker who identified herbivore dung in a 10 m long, 2 m wide, belt transect centred on the tick drag transect. Any

Table 1. Vegetation characteristics of each burn age. Sward height was determined using the direct measurement method described in Stewart et al. (2001); species composition and the percentage of palatable grasses (decreasers) was based on veld condition index method (Hardy et al. 1999).

Burn age	Time since burn (years)	Mean sward height (cm)	No. of grass species	Palatable grasses	Dominant grass species (in descending order)
2010	5	124	21	5%	herringbone <i>Pogonarthria squarrosa</i> ; common russet <i>Loudetia simplex</i> ; gum <i>Eragrostis gummiflua</i> ; wool <i>Antheophora pubescens</i>
2011	4	92	23	5%	herringbone <i>Pogonarthria squarrosa</i> ; common russet <i>Loudetia simplex</i> ; broad curly leaf <i>Eragrostis rigidior</i> ; red autumn <i>Schizachyrium sanguineum</i>
2012	3	65	18	7%	common russet <i>Loudetia simplex</i> ; red autumn <i>Schizachyrium sanguineum</i> ; herringbone <i>Pogonarthria squarrosa</i> ; broad curly leaf <i>Eragrostis rigidior</i>
2013	2	28	20	9%	greater spear <i>Trachypogon spicatus</i> ; red grass <i>Themeda triandra</i> ; gum <i>Eragrostis gummiflua</i> ; spear <i>Heteropogon contortus</i>
2014	1	<5	24	17%	red <i>Themeda triandra</i> ; narrow curly leaf <i>Eragrostis chloromelas</i> ; red autumn <i>Schizachyrium sanguineum</i> ; wire <i>Elionurus muticus</i>

fresh dung (i.e. that thought to have been deposited within the previous 72 h taking into account insect activity and moisture levels) was identified to species level. It was not possible to determine the number of animals that had produced any given dung pile with any degree of confidence and thus data were collected on presence rather than abundance. Dung evidence was used to estimate herbivore numbers because this was the only way to directly link tick numbers and herbivores in exactly the same area. Direct surveys such as large mammal transects are very effective for recording the presence of animals over a large area (e.g. over an entire burn block) but it would not have been suitable for assessing herbivore presence in the specific tick sample transects. Although using dung as a proxy for herbivore presence is not without challenge (animals can be present without defecating and detection of dung can be difficult in high swards), it does provide a conservative estimate of herbivore presence at very precise spatial scales (Sutherland 1996) including in African ecosystems (Plumptre 2000, Radloff 2008).

Statistical analysis

A generalised linear mixed model analytical framework was used to analyse the tick data. Two fixed factors were entered – 1) burn age (n=5) and 2) block identity (n=16) – together with site (n=48) as a random factor. To reflect the study approach, we used a nested design (10 drags per site, 3 sites per block, 3–4 blocks per burn). For the data on tick abundance, we entered either number of larvae or number of nymphs as the response variable and specified a Poisson error term with a log link function. Three candidate models were then created: 1) Site(Block) to test for differences between the blocks without burn age being factored in; 2) Site(Burn) to test for differences between the burn ages without the different blocks being factored in (i.e. a uniform effect of burning between the block); and 3) Site(Burn×Block) to test for the effects of an interaction between block and burn age (i.e. to test for block-specific effects of burning). The three candidate models were compared using delta Akaike's information criterion (Δ AIC) values for model fit and p-values for model significance. The same approach was used for data on tick presence/absence using a binomial error term with a logit link function. All statistics were calculated in SPSS ver. 22.

Results

Ticks were found on 182 of the 480 tick drags (37.9%), versus 298 drags (62.1%) that were tick-free. Of those transects with ticks, 152 (83.5%) had only larvae, 16 (8.8%) had only nymphs, and 14 (7.7%) had both. In total, 1598 larvae and 131 nymphs were found; all individuals were Ixodidae (hard ticks) but were not identified to genus/species. There was no relationship between the number of ticks in larval and nymph life stages found in each block burn area and the size of that area (Pearson correlation: $r=0.121$, $n=16$, $p=0.655$ and $r=0.001$, $n=16$, $p=0.997$, respectively). No adult forms were found on the tick drag during the study, but adult forms were present throughout the site and were observed on human, domestic dog and antelope hosts.

The binomial GLMMs for tick presence showed that the presence/absence of ticks at different sampling sites was significantly affected by burn age and block when these factors were entered into separate candidate nested models; this was true for both larval and nymph stages ($p < 0.001$ in all cases; Table 2). However, for both lifestages, the optimal model was that which allowed for the interaction between burn age and block (AIC much lower than the candidate models with these factors included in isolation; $p < 0.001$ and $p = 0.003$, respectively; Table 2). The Poisson GLMMs for tick abundance showed a similar (Table 2), but more dramatic, pattern with models for larvae and nymphs that just included burn or block being significant, but the optimal models in both cases being Site(Burn×Block) (lower AIC; more significant).

The above patterns were driven by a fundamental effect of burn age on tick presence and abundance. Tick larvae and nymphs were more prevalent in blocks that had been burned two or three years before the study in comparison with blocks burned either the preceding year or much longer ago (four or five years previously) (Fig. 2a–b). A similar pattern was seen for tick abundance, with larval abundance being highest in blocks that had been burned two or three years before the study relative to recent burns and old burns (Fig. 3a). The pattern for nymph abundance was similar although in this case abundance was highest in blocks burned two years previously followed by a tie for blocks burned one or three years previously; as previously for larvae, blocks burned 4–5 years ago were associated with the lowest tick abundance (Fig. 3b).

Table 2. GLMM nested models of the presence and abundance of tick larvae and nymphs. For each dependent variable, three candidate models were compared using delta Akaike's information criterion (Δ AIC) to examine the effects of: 1) burn age (defined as number of years since last burn from 1 to 5); 2) individual block (n=16; 3–4 for each burn age); and the interaction between burn age and block to account for local (block-level) differences in the effect of burning on ticks.

Dependent	Model	Wald	df	p	Δ AIC
Larval presence	Site(Block)	77.333	15	<0.001	44
	Site(Burn)	67.298	18	<0.001	43
	Site(Burn×Block)	83.937	48	<0.001	0
Larval abundance	Site(Block)	7187.235	15	<0.001	1558
	Site(Burn)	8177.476	18	<0.001	1168
	Site(Burn×Block)	11322.498	44	0.001	0
Nymph presence	Site(Block)	145.233	15	<0.001	15
	Site(Burn)	157.717	18	<0.001	34
	Site(Burn×Block)	78.723	48	0.003	0
Nymph abundance	Site(Block)	78.419	15	<0.001	149
	Site(Burn)	67.173	18	<0.001	158
	Site(Burn×Block)	262.451	44	<0.001	0

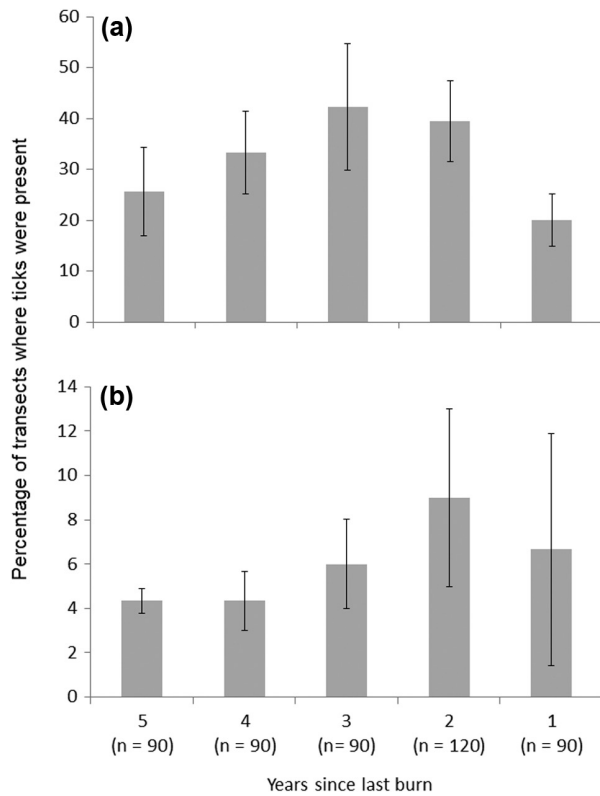


Figure 2. Mean percentage of tick drags in each burn age where ticks were present in: (a) larval life stage; or (b) nymph life stage. Error bars show SEM. n = number of tick drags conducted; each tick drag covered 20 m².

The optimal model in all cases was generated when the interaction between burn age and block was analysed. This indicates that relationship between burning and tick presence/abundance is not straightforward and that burn age and block together influence tick numbers. Indeed, it is notable that, for both presence and abundance, mid-burn areas had the highest inter-block variability in most cases, except for nymph presence where the highest inter-block variability was in the most recent burn blocks (Fig. 2, 3). This suggests that habitat heterogeneity is an important modifier of the effect of burning on tick numbers.

Based on dung evidence, there was a significant difference in herbivore presence between the different burn ages. Table 3 shows presence of dung of the 14 different species of medium-to-large herbivores found during surveying. There was a significant difference in the frequency of dung (all species combined) between the different burn ages ($\chi^2 = 27.188$, $df = 4$, $p < 0.001$). This was driven by higher presence of herbivores in the more recent burns (Table 3). There was also a significant positive correlation between the number of ticks and the number of herbivore species present at each sample point based on dung evidence (Spearman rank test: $r_s = 0.109$, $n = 450$, $p = 0.021$), with 21% of the variation in tick numbers explained by dung data.

Discussion

Our opposing hypotheses predicted that ticks should be less prevalent and less abundant either in the most recently

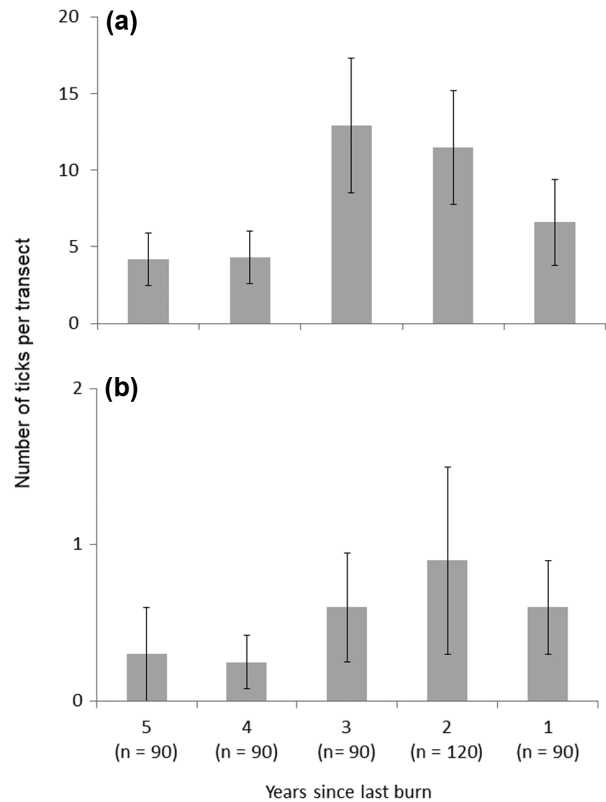


Figure 3. Mean abundance of ticks in each burn age in: (a) larval life stage; or (b) nymph life stage. Error bars show SEM. n = number of tick drags conducted; each tick drag covered 20 m².

burned areas or in those areas that were burned a long time previously. However, our results showed that while tick presence was related to burning, the relationship was not linear in either direction. Presence of larvae and nymphs was actually lowest in grassland blocks burned within the preceding year (20% and 6%, respectively) and those that had not been burned for the last five years (25% and 4%, respectively), supporting both hypotheses. The highest tick presence occurred in grassland burned three years or two years previously, where larval ticks were found in 42% and 40% of all sampling transects respectively and nymphs were found in 7% and 9%, respectively. Findings were similar for abundance, with the highest numbers being in the mid-stage burn blocks. The bell-shaped curvilinear relationship between burn age and tick presence/abundance is not predicted by either of the hypotheses tested but can be explained by both in combination. It should be noted that this study was based on data from one reserve sampled in a single season (autumn) of one year. Consequently our findings, although valid statistically and biologically, should be empirically tested at longer temporal scales, and at multiple sites, before the generality of conclusions drawn can be confirmed.

The lack of ticks in recently-burned areas is likely to be partly because of ticks being killed directly by the fire and unable to recover in the intervening time (Scrifers et al. 1988). It was also notable that the sward height in areas burned the preceding year was extremely low (ca 2 cm; partly as a result of drought conditions that had affected regrowth: Table 1), offering very limited refugia for desiccation-vulnerable

Table 3. Presence of dung of the 14 species of medium-to-large herbivores found during surveying expressed as the number of tick drag transects where dung of each species was encountered. Total dung is a simple sum of the species-specific information. Dung information was collected from 90 tick drags per burn.

Years since burn	Zebra	Wildebeest	Blesbok	Impala	Warthog	Giraffe	Eland	Kudu	Tsessebe	Red Hartbeest	Waterbuck	Rhino	Gemsbok	Reedbuck	Total dung
5	46	12	4	8	1	3	6	4	3	0	3	2	7	0	100
4	32	11	2	8	22	10	3	8	0	0	0	2	1	0	100
3	38	12	16	7	20	11	8	3	1	1	4	4	0	2	140
2	63	24	10	7	4	12	9	6	2	1	0	1	0	2	130
1	65	33	26	29	0	1	10	7	13	10	4	2	0	2	170

ticks (Gray 1991, Fyumagwa et al. 2007, Polito et al. 2007, del Fabbro et al. 2015). A similar result was also found by Fyumagwa et al. (2007) in Tanzania and at some (but not all) sites in South Africa by Spickett et al. (1992). It should also be noted that the presence of the drought itself resulted in drier conditions, which might have had a negative effect on tick populations throughout the reserve.

The lack of ticks in areas burned four or more years previously can likely be explained by a relative absence of suitable large animal hosts in these areas. This is supported by the lowest levels of herbivore presence in the oldest burns based on dung data (Table 3) and has been noted previously (Gureja and Owen-Smith 2002, Parrini and Owen-Smith 2010). This pattern is driven by old burn areas becoming dominated by rank grasses with low palatability and poor nutritional value (Hardy et al. 1999), and is evident at the study site with fewer palatable species in older burns (Table 1). This lack of ticks in old burn areas might be a direct effect of habitat change or might be indirect as a result of herbivore hosts moving away from such sites. In contrast, the comparatively high tick presence and abundance for blocks burned two or three years previously provides an intermediate state: habitat containing tick refugia and high levels of herbivore hosts. This explanation is supported by high herbivore presence in the later burns and by the positive correlation between herbivore presence and the number of ticks. This concurs with studies by Allan (2009) and Adams et al. (2013) in the very different environment of North American woodland and suggests that the time taken for tick re-invasion of burned areas is around two years post burning. Re-invasion is likely to involve animals transporting ticks back into such habitat as they seek palatable grasses (Spickett et al. 1992). Given that immature ticks also feed on smaller hosts (Durden 2006, Padgett et al. 2009) the distribution of mammals such as scrub hare *Lepus saxatilis* and springhare *Pedetes capensis* could also have a strong influence on tick abundance that would typically be unrecognised as survey attention understandably tends to focus on economically significant (and more readily surveyed) large mammal species. We suggest that accounting for the presence of small mammals in relating tick numbers to habitat and management would be a useful avenue for future study.

For both larvae and nymphs, there was a strongly significant interaction between burn age and the individual block within that burn age. This suggests that underlying habitat heterogeneity influences how burn management will affect tick numbers. A similar conclusion was reached by Spickett et al. (1992), who found that the exact time needed for tick abundance recovery is variable and dependent upon local conditions. Similarly, Schulz et al. (2014) found that high localised heterogeneity in habitat affected ticks, especially when this affected relative humidity and especially ground temperature, played a vital role in the dynamics of tick populations and their activity. Parr and Anderson (2006) have also highlighted that between-patch variability in both biotic and abiotic parameters can be substantial even within the same burn age. In our study, one of the big habitat modifiers is likely to be location of waterholes, which fundamentally affects animal distribution in a way that is completely separate to the burning regime. It is

notable that at our study site, there are waterholes within, or adjacent to, each block but would be interesting to examine any subtle effects of distance to water on tick populations, and the way that this might interact with the effects of burning, in future research. Such research could also incorporate other environmental factors such as microclimate and soil characteristics.

The absence of any adult ticks in the samples was unexpected. It is possible that this reflects a sampling bias, although tick drags are widely used to sample adult ticks as well as immature stages (Tack et al. 2011). It is thus more likely that absence of adult ticks is a seasonal effect; a study of tick seasonal abundance in South Africa showed that adult ticks are often absent in autumn (especially May when this study was undertaken) and that larvae are the dominant life stage sampled (Rechav 1982). It should be noted that, in this study, ticks were not identified but future studies could be usefully extended by including analyses of individual species to account for species-specific seasonality and effects of burning (e.g. some species using soil refugia to escape fire: Padgett et al. 2009).

Overall, our results suggest that fire likely has an effect on tick presence/abundance and could potentially be better harnessed as a tick control mechanism. Rotational burning is primarily undertaken to create a habitat mosaic and maintain an adequate food supply at all times so it would not be feasible to burn whole reserves annually to control ticks. However, consideration should be given to regular annual burning of areas where animals congregate in large numbers, such as around key water holes. Such 'tick control burns' could also be optimised seasonally so that they occur in late dry season as recommended by Fyumagwa et al. (2007) rather than after the first rains as is recommended for burns where the primary aim is management of grassland condition (Trollope 1990).

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References

- Adams, J. et al. 2013. Effects of prescribed burning on small mammal, reptile, and tick populations on the Talladega National Forest, Alabama. – In: Guldin, J. M. (ed.), Proc. 15th Bienn. southern silvicultural research conference. Dept of Agriculture, Forest Service, Southern Research Station. pp. 123–126.
- Allan, B. F. 2009. Influence of prescribed burns on the abundance of *Amblyomma americanum* (Acari: Ixodidae) in the Missouri Ozarks. – J. Med. Entomol. 46: 1030–1036.
- Brown, K. et al. 2013. Animal disease and the limits of local knowledge: dealing with ticks and tick-borne diseases in South Africa. – J. R. Anthropol. Inst. 19: 319–337.
- Bryson, N. R. et al. 2000. Collection of free-living nymphs and adults of *Amblyomma hebraeum* (Acari: Ixodidae) with pheromone/carbon dioxide traps at 5 different ecological sites in heartwater endemic regions of South Africa. – Exp. Appl. Acarol. 24: 971–982.
- Cully, Jr, J. F. 1999. Lone star tick abundance, fire and bison grazing in tallgrass prairie. – J. Range Manage. 52: 139–144.
- del Fabbro, S. et al. 2015. Investigating the relationship between environmental factors and tick abundance in a small, highly heterogeneous region. – J. Vector Ecol. 40: 107–116.
- Drew, M. L. et al. 1985. An evaluation of burning for control of winter ticks, *Dermacentor albipictus*, in central Alberta. – J. Wildl. Dis. 21: 313–315.
- Durden, L. A. 2006. Taxonomy, host associations, life cycles and vectorial importance of ticks parasitizing small mammals. – In: Morand, S. et al. (eds), Micromammals and macroparasites. Springer, pp. 91–102.
- Fyumagwa, R. D. et al. 2007. Ecology and control of ticks as disease vectors in wildlife of the Ngorongoro Crater, Tanzania. – S. Afr. J. Wildl. Res. 37: 79–90.
- Gleim, E. R. et al. 2014. The phenology of ticks and the effects of long-term prescribed burning on tick population dynamics in southwestern Georgia and northwestern Florida. – PLoS One 9: e112174.
- Gray, J. S. 1991. The development and seasonal activity of the tick *Ixodes ricinus*: a vector of Lyme borreliosis. – Rev. Med. Vet. Entomol. 79: 323–333.
- Groombridge, B. 1992. Global biodiversity: status of the Earth's living resources. – Chapman and Hall.
- Gureja, N. and Owen-Smith, N. 2002. Comparative use of burnt grassland by rare antelope species in a lowveld game ranch, South Africa. – S. Afr. J. Wildl. Res. 32: 31–38.
- Hardy, M. B. et al. 1999. Veld condition assessment. – In: Tainton N (ed.), Veld management in South Africa. Pietermaritzburg. Univ. of Natal Press, pp. 194–216.
- Hoch, A. et al. 1972. Preliminary observations on controlled burning for lone star tick (Acarina: Ixodidae) control in woodlots. – J. Med. Entomol. 9: 446–451.
- Horak, I. G. et al. 2006. Effect of burning on the numbers of questing ticks collected by dragging. – Onderstepoort J. Vet. Res. 73: 163–174.
- Jongejan, F. and Uilenberg, G. 2004. The global importance of ticks. – Parasitology 129: S3–S14.
- Kivaria, F. M. 2006. Estimated direct economic costs associated with tickborne diseases on cattle in Tanzania. – Trop. Anim. Health Prod. 38: 291–299.
- Latif, A. A. and Walker, A. R. 2004. An introduction to the biology and control of ticks in Africa. – Int. Consortium on Ticks and Tick Borne Diseases (ICTTD-2) project 1-29.
- Madder, M. et al. 2015. Ticks. – Report, Univ. of Pretoria and Afrivet.
- Martin, R. E. and Sapsis, D. B. 1992. Fires as agents of biodiversity: pyrodiversity promotes biodiversity. – In: Kerner, H. M. (ed.), Proc. Symp. on biodiversity in northwestern California, 1991. Wildland Resources Centre, Univ. of California, Berkeley, pp. 150–157.
- Moore, W. 1912. The tick problem in South Africa. – J. Econ. Entomol. 5: 377–384.
- Moyo, B. and Masika, P. J. 2009. Tick control methods used by resource-limited farmers and the effect of ticks on cattle in rural areas of the eastern Cape Province, South Africa. – Trop. Anim. Health Prod. 41: 517–523.
- Padgett, K. A. et al. 2009. Effect of prescribed fire for tick control in California chaparral. – J. Med. Entomol. 46: 1138–1145.
- Parr, C. L. and Brockett, B. H. 1999. Patch-mosaic burning: a new paradigm for savanna fire management in protected areas? – Koedoe 42: 117–130.
- Parr, C. L. and Andersen, A. N. 2006. Patch mosaic burning for biodiversity conservation: a critique of the pyrodiversity paradigm. – Conserv. Biol. 20: 1610–1619.
- Parrini, F. and Owen-Smith, N. 2010. The importance of post-fire regrowth for sable antelope in a southern African savanna. – Afr. J. Ecol. 48: 526–534.
- Pfitzer, S. et al. 2011. Tick-borne blood parasites in nyala (*Tragelaphus angasi*, Gray 1849) from KwaZulu-Natal, South Africa. – Vet. Parasitol. 176: 126–131.

- Plumptre, A. J. 2000. Monitoring mammal populations with line transect techniques in African forests. – *J. Appl. Ecol.* 37: 356–368.
- Polito, V. J. et al. 2013. Tick abundance and levels of infestation on cattle in response to patch burning. – *Rangeland Ecol. Manage.* 66: 545–552.
- Radloff, F. G. T. 2008. The ecology of large herbivores native to the coastal lowlands of the Fynbos Biome in the Western Cape, South Africa. – PhD thesis, Stellenbosch Univ., South Africa.
- Rechav, Y. 1982. Dynamics of tick populations (Acari: Ixodidae) in the eastern Cape Province of South Africa. – *J. Med. Entomol.* 19: 679–700.
- Schulz, M. et al. 2014. Abundance and seasonal activity of questing *Ixodes ricinus* ticks in their natural habitats in southern Germany in 2011. – *J. Vector Ecol.* 3: 56–65.
- Scrifes, C. J. et al. 1988. Gulf coast tick (*Amblyomma maculatum*) populations and responses to burning of coastal prairie habitats. – *Southwest. Nat.* 33: 55–64.
- Sonenshine, D. E. 1991. *Biology of ticks*. Vol. I. – Oxford Univ. Press.
- Spickett, A. M. et al. 1992. The effect of veld-burning on the seasonal abundance of free-living ixodid ticks as determined by drag-sampling. – *Onderstepoort J. Vet. Res.* 59: 285–292.
- Stafford III, K. C. et al. 1998. Impact of controlled burns on the abundance of *Ixodes scapularis* (Acari: Ixodidae). – *J. Med. Entomol.* 35: 510–513.
- Stewart, K. E. J. et al. 2001. An evaluation of three quick methods commonly used to assess sward height in ecology. – *J. App. Ecol.* 38: 1148–1154.
- Steyl, J. C. et al. 2012. Theileriosis (Cytauxzoonosis) in Roan antelope (*Hippotragus equinus*): field exposure to infection and identification of potential vectors. – *Onderstepoort J. Vet. Res.* 79: 1–8.
- Sutherland, W. J. 1996. *Ecological census techniques* – Cambridge Univ. Press.
- Tack, W. et al. 2011. The effects of sampling method and vegetation type on the estimated abundance of *Ixodes ricinus* ticks in forests. – *Exp. Appl. Acarol.* 54: 285–292.
- Trollope, W. S. W. 1990. Veld management with specific reference to game ranching in the grassland and savanna areas of South Africa. – *Koedoe* 33: 77–86.
- Walker, A. R. et al. 2003. *Ticks of domestic animals in Africa: a guide to identification of species*. – Bioscience Reports, Univ. of Edinburgh.
- West, O. 1965. *Fire in vegetation and its use in pasture management with special reference to tropical and subtropical Africa*. – Commonwealth Agricultural Bureaux.
- Wilkinson, P. R. 1979. Ecological aspect of pest management of Ixodid ticks. – *Recent Adv. Acarol.* 2: 25–33.
- Wynberg, R. 2002. A decade of biodiversity conservation and use in South Africa: tracking progress from the Rio Earth Summit to the Johannesburg World Summit on Sustainable Development. – *S. Afr. J. Sci.* 98: 233–243.