Can the Potential for Tick Infestation Influence Patterns of Resource Use by Eland (*Taurotragus oryx*)?

By

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DECLARATION

I declare that this thesis is my own, unaided work. It is being submitted for the Degree of Master of Science in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any other University.

Doug McCulloch
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Dedicated to Alan Batchelor

1949-2012

A wise and inspirational mentor;

A kind and loyal friend;

A brave and gifted naturalist

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LIST OF ACRONYMS

The following table contains a list of acronyms used in the text to streamline the document.

Term	**Acronym**
Kgaswane Mountain Reserve	KMR
North West Parks and Tourism Board	NWPTB
Short Upland Grassland	SUG
Tall Upland Grassland	TUG
Tall Lowland Grassland	TLG
Shrubland; Tall Grass Layer	ST
Tall Closed Woodland	TCW
Tall Open Woodland; Tall Grass Layer	TOW(T)
Tall Open Woodland; Short Grass Layer	TOW(S)
Kruskal-Wallis Test	KW
Wilcoxon's Signed Rank Test	WSR
Chi-Squared Test	χ^2

ABSTRACT

The vegetation of the Kgaswane Mountain Reserve, in North West Province, South Africa, was mapped according to seven vegetation structure types, based on tree density and height, and grass height. Free-living ticks were collected by drag-sampling the vegetation from each structure type in November 2014, prior to the onset of the summer rains, and February 2015, once most of the seasonal rains had fallen. Eland (*Taurotragus oryx*) location information was recorded from four GPS collared cows over the two sample periods. Tick abundance was consistently lower in shorter, open, more exposed vegetation structure types, and higher in more sheltered types. Position higher up in the landscape nullified the positive impacts of trees on beneath-canopy microclimate in tall open woodlands, as indicated by comparatively lower tick numbers than in more sheltered woodland types. Tick abundance is influenced by vegetation structure and the availability of hosts. The majority of ticks trapped during both periods were larvae, with nymphs mostly present in November and adults mostly present later in the season, indicating the seasonal nature of tick cohort recruitment. Eland calving behaviour centred on areas with low adult tick abundance. Eland did not respond to total tick abundance during either sampling period. They did select areas with low adult tick abundance, and avoided areas with high adult tick abundance. This corresponded with an improvement in upland forage quality, which allowed them to avoid foraging in areas with high adult tick abundance. It is plausible that the potential for infestation by adult ticks may be a supplementary influence driving the use of space by eland.

Keywords: North West Province; vegetation structure, tick abundance, eland, calving, drag-sampling.

1. AIM OF THE STUDY

The aim of this study is to investigate the relationships between vegetation structure, tick abundance and patterns of eland (*Taurotragus oryx*) movement across a season within a small nature reserve.

2. RESEARCH OBJECTIVES

Objective 1: To investigate the relationship between vegetation structure and tick abundance.

Objective 2: To examine the influence of vegetation structure on the occurrence of the different stages of development of ticks, namely larvae, nymphs and adults, between the two sample periods.

Objective 3: To examine patterns of diurnal tick activity between early summer prior to the bulk of the rainfall, and later summer after most rainfall has occurred.

Objective 4: To investigate the potential for tick abundance to influence temporal patterns of resource use by eland.

3. GENERAL INTRODUCTION AND LITERATURE REVIEW

3.1 Motivation for the Study

During a study investigating the seasonal dietary preferences of eland at the Kgaswane Mountain Reserve (KMR), a colleague remarked at the high level of tick infestation observed on the animals. This initiated the question: in the absence of predators and tick control mechanisms such as oxpeckers (*Buphagus spp.*), is the challenge exerted by ticks great enough to influence the patterns of resource use by eland?

We live in a dynamic period within a dynamic continent. There is substantial evidence to support changes in global climate attributable to a collective economic dependence on fossil

fuels (Parmesan and Yohe, 2003; Root *et al*., 2003; Thomas *et al.*, 2004; Hannah, 2010; Richardson *et al.*, 2009). Already in instances where low temperature is a dominant controlling variable, we are seeing marked changes in the balance between various ecosystem components resulting in complete ecosystem transformation. An example is the outbreak of pinebark beetle infestations in the coniferous forests of the north-western United States (Rosner, 2015). Climatic changes are likely to manifest unevenly across the globe, and considerable debate remains surrounding the nature of these manifestations. Semi-arid regions are predicted to be subject to a more extreme frequency of stochastic climatic events, higher mean temperatures and overall desiccation (Scholes *et al*., 2008; Richardson *et al.*, 2009).

Climatic changes coupled with elevated atmospheric carbon levels may result in changes to vegetation structure in several ways. Warmer, semi-arid conditions tend to favour the distribution of C4 rangelands (tall, stemmy, sub-tropical grass species) over C3 rangelands (short, finely tufted, temperate grass species) (Gibbs-Russel *et al*., 1990; Beerling and Osborne, 2006; Bond, 2008). Increased temperature and elevated atmospheric carbon dioxide concentration may favour the increased growth of woody vegetation at the expense of herbaceous vegetation (Bond and Midgely, 2000; Bond, *et al*., 2003). There may also be changes in structure within graminoid communities associated with altered environmental conditions at the landscape and local scales, such as the favouring of tall, stemmy, unpalatable *Andropogonoid* grass species over *Panicoid* grasses (softer, palatable, medium-sized species) (Gibbs-Russell, 1990; Scholes, 1998; Bond *et al.*, 2003). Rangelands are strongly influenced by herbivores and fire (O'Connor and Bredenkamp, 1997; Scholes and Archer, 1997; Bond, 2008).

Tree density is an integral component of vegetation structure because it adds height, which has the potential to modify localized climatic variables leading to the physical and environmental stratification of niches that constitute an ecosystem. Tree density in savannas is controlled predominantly by top-down and bottom-up effects. Top-down effects are fire and herbivory, which consume vegetation, open patches and suppress tree recruitment (Bond and Keeley, 2005; Bond, 2008; Sankaran *et al*., 2008). Bottom-up controls concern limitations on resources, which may be inherent or created by below-ground competition between root systems. In semi-arid rangelands where there is no spatial separation of tree and grass root niches, the root systems of the grass sward exert a strong suppressive influence on tree seedling recruitment by competing for limiting resources such as moisture and nitrogen (Scholes and Walker, 1993; Scholes and Archer, 1997; Sankaran *et al*., 2005; Bond, 2008).

There is inherent structural variation in the herbaceous layer of semi-arid rangelands, also guided by top-down and bottom-up effects. Shallow, rocky, sandy soil may create limitations on moisture and nutrients, leading to a short, dense sward while the higher water holding capacity and nutrient status of deeper, heavier soils is conducive to the formation of a sward dominated by tall, robust species (Scholes and Walker, 1993; Scholes, 1998). Fire acts as a non-selective grazer, temporarily and suddenly converting a tall, dense sward into a short sward (Scholes, 1998; Uys *et al*., 2004). Large herbivores physically alter the sward as they move through it, by grazing, trampling or both (McNaughten, 1979; Caughley, 1982). They are also responsible for the localized distribution of nutrients across the landscape, leading to the heterogenous distribution of resources (Caughley, 1982; Tainton, 1999).

Rainfall and soil moisture are primary determinants of herbaceous biomass production and accumulation in southern African rangelands (Tainton and Walker, 1993; O'Connor and Bredenkamp, 1997; Scholes, 2003; Uys *et al*., 2004). The rate and volume of biomass accumulation in turn determines the frequency and intensity of fires (Scholes, 1998; Bond and Loffell, 2001; Bond and Keeley, 2005). Intense fires are responsible for elevated seedling die-off and stunting, keeping short trees within the "fire-trap" and maintaining a more open savanna structure (Walker, 1987; Scholes and Archer, 1997; Scholes, 1998; Bond and Keeley, 2005; Bond, 2008). Rainfall, and more precisely aridity, is also an important driver of woody plant biomass and species composition (Scholes *et al*., 2002), and is hence an important determinant of savanna vegetation structure.

It is clear that, given the influence of climate on the fundamental ecological processes that govern vegetation structure, the distribution of current plant communities is likely to shift as ecosystems respond to new climate regimes. Profound changes to the structure of vegetation may have attendant ecological impacts, such as influencing the distribution and abundance of ticks (Gray *et al*., 2009; Gilbert, 2010; Medlock *et al*., 2013). This is occurring in tandem with unprecedented growth in the game farming industry in South Africa, which is seen as a more profitable, lower-risk economic alternative to conventional livestock farming (Van der Merwe *et al*.; 2003; Dry 2010; Mail and Guardian 2012; Moneyweb 2013). The result is the proliferation of high-income, high-investment game and wildlife farming agribusinesses on properties that are comparatively small and management-intensive. Understanding the drivers of tick abundance within management units that are subject to external influences, and the potential influence this may exert on patterns of animal resource use, may have economic applications.

3.2 Life History Strategies of Ticks (the Acarina)

Most game species from different parts of South Africa carry high tick burdens (Bothma, 1993). As a general rule antelope up to the size of a blue wildebeest carry mostly immature ticks and those larger than blue wildebeest carry both immature and mature ticks in large numbers (Bothma, 1993). Ticks find their hosts mainly by questing, or attaching themselves to vegetation and waiting to intercept a passing host (Walker *et al.*, 2003; Medlock *et al.*, 2013). The adults of the *Amblyomma* and *Hyalomma* genera are more proactive, actively crawling across the ground in search of a host. This is known as exophilic behavior (Walker *et al.*, 2003).

Ticks have a relatively simple life cycle. The adult, fully engorged female falls from the host and lays eggs in an appropriate refuge on the ground. The eggs hatch, and the larvae climb onto adjacent grass stems to await passing hosts (Walker *et al*., 2003). In the case of one-host species such as the blue tick (*Boophilus spp*), eggs are laid on the ground. The larva moults on the host into a nymph and re-attaches to the same host to engorge. The nymph then moults on the host into an adult and remains on the same host until engorged once again (Monnig and Veldman, 1984; Bothma 1993; Walker *et al.*, 2003). Hence all feedings and subsequent moults of an individual tick take place on the same host. The life-cycle is rapid, taking three weeks for feeding and two months for egg laying and larval development (Walker *et al.*, 2003).

In the case of the two-host tick, such as bont-legged ticks (*Hyalomma* spp), the larva attaches, engorges and moults into a nymph on the first host. The engorged nymph falls off the host and moults into an adult on the ground. The adult then awaits a second host to complete the life cycle (Monnig and Veldman, 1984; Walker *et al.*, 2003). The larvae and nymphs of the bont-legged ticks usually feed on smaller mammals and birds, with only the adults found on large mammals. These are aggressive parasites, actively searching for hosts, and are resistant to drought (Monnig and Veldman, 1984; Walker *et al.*, 2003). The modification to the life cycle may be a strategy aimed at surviving droughts since the time spent away from the host is reduced.

Three-host ticks have three separate hosts, one for each stage, with moulting occurring on the ground (Monnig and Veldman, 1984; Bothma 1993; Walker *et al.*, 2003). This is the most common type of life cycle (Walker *et al*., 2003). Ticks that have recently hatched or moulted are soft-bodied and are inactive for one to two weeks until their bodies have hardened. The life-cycle of three-host ticks is slow, from six months to several years.

The scale and scope of the project left little opportunity to identify the ticks to genus level. The proportion of the captured tick population represented by each life history strategy was undetermined. Larvae remain aggregated whilst waiting for a host (Medlock *et al*., 2015), and life history information would have provided valuable insight into the patterns of tick dispersal by hosts following hatching. Three-host tick species spend the most time away from the host, and are hence likely to be the most vulnerable to off-host mortality due environmental factors. Since the three-host life cycle is the most common, it was assumed that this was the dominant strategy adopted by the ticks encountered. My study focused on tick abundance, and hence although data on life history strategy is deemed useful, they were not considered central to the objectives of the project.

3.3 Drivers of Tick Abundance

My study is confined to questing ticks, which adopt an ambush technique by climbing up vegetation and waiting for a host to brush past (Medlock *et al*., 2013). The literature is generally consistent in identifying temperature, relative humidity, rainfall and evaporation as key variables governing such parameters as tick mortality; tick activity; tick distribution; tick abundance and tick growth rates, albeit to varying degrees (Dipeolu, 1989; Needham and Teal, 1991; Randolph, 1997; Estrada-Pena, 2001; Cumming, 2002). Density independent mortality at the female to larval stage is correlated with particular climatic factors, namely minimum temperature and minimum relative humidity (Dipeolu, 1989; Randolph, 1997). The development period, i.e. tick growth rate, is most rapid at high temperatures (30^{o}C) and is at its longest at cooler temperatures, these being approximately 12^{o}C and lower (Randolph, 1997).

Water balance is also of key importance in tick survival (Needham and Teal, 1991; Gray *et al*., 2009; Gilbert, 2010; Medlock *et al*., 2013). During questing the tick is prone to drying out, and so descends the vegetation into the litter layer or grass tuft bases to rehydrate (Medlock *et al*., 2013). This cycle of dehydration/ rehydration and moving up and down the vegetation reduces the opportunity of host interception and uses up important energy resources, and is deemed detrimental to off-host tick survival. The moisture content of the ground-based vegetation, and the shelter from desiccation it provides, is hence an important component of tick survival (Medlock *et al*., 2013). Ticks that have moulted are particularly vulnerable to desiccation, starving and freezing because their exoskeletons have not yet hardened (Walker *et*

al., 2003), and the ratio of body volume to body surface area against the prevailing environmental variables adopts increasing importance (Lovegrove, 1993). While growth periods are largely temperature mediated, tick mortality is seen as the result of a complex of integrated climatic relationships. Tick survival and reproduction are dependent on the covariance between temperature and rainfall, rather than a single variable alone (Cumming, 2002).

Ticks exhibit a peak seasonal abundance, with the largest number of larvae occurring in autumn and winter, nymphs during winter and spring and adults during summer (Bothma, 1993; Zeiger *et al*., 1998). Tick recruitment hence occurs in cohorts, with the seasonal dynamics of tick activity closely tied to the timing of questing activity of desiccation-vulnerable larvae (Randolph, 1993; Medlock *et al.,* 2013). The timing of activity of nymphs and adults is dependent on temperature (Randolph, 1993; Randolph, 1997). The most important environmental factor appears to be night-time minimum temperature, determining condensation and saturation deficit and thus the ticks' ability to replenish moisture lost during the daytime and so to survive while questing for hosts (Randolph, 1993). Larvae numbers are correlated most closely with these factors (Randolph, 1993; Randolph, 1997).

In terms of tick abundance, model results have shown a statistically significant positive influence of increasing mean annual temperature and a negative influence of increasing number of frost days (Ruiz-Fons *et al*., 2012). Ticks do not survive frosts (Walker *et al.,* 2003). Minimum temperature, maximum temperature and rainfall are also the most important factors in predicting tick distribution (Cumming, 2002; Medlock *et al*., 2008; Gilbert, 2010; Medlock *et al*., 2013). The key to describing tick occurrence is the covariance of temperature and rainfall. Each of the following variables is potentially a limiting factor in tick distribution: vegetation type, plant productivity, elevation, maximum temperature, minimum temperature and rainfall (Cumming, 2002; Estrada-Pena, 2008; Medlock *et al*., 2008; Gilbert, 2010; Medlock *et al*., 2013). Cumming (2002) found that climate was a better predictor for tick distribution than vegetation, suggesting that climatic factors exerted more control on tick populations than habitat physical features. This study was, however, carried out at a continental scale where the key vegetation parameter was vegetation type, rather than the structure of the plant communities within the broader matrix. Most modeling of the environmental determinants of tick distribution occurs at the landscape scale (Randolph, 1997; Estrada-Pena, 2008; Medlock *et al*., 2008; Scharlemann *et al*., 2008; Medlock *et al*., 2013). Cumming (2002) concedes that vegetation structure may well be an important determinant at the local scale.

Related to this, short, open grasslands have been found to be unsuitable habitat for the free-living stages of most ticks (Londt & Whitehead 1974; Short *et al*.. 1989a). In a study undertaken in central Zambia, Zeiger *et al.* (1998) found that woodland supported mostly adult ticks, while nymphs were located mostly in open grasslands. Tick survival is affected by microclimate, and protection from sunlight, frost or fire (Londt & Whitehead 1974; Short *et al.*, 1989a). Longer grasslands ostensibly provide more favourable microclimates for the free-living stages of ticks, and these habitats also support larger populations of small mammals and ground birds, important hosts for the immature stages of many ticks (Horak, *et al*.. 1991b; Horak *et al*. 1991c; Walker 1991; Medlock *et al*., 2013). Short grasses are also likely to limit the questing height of the ticks.

Tick abundance has been shown to be strongly influenced by the number of hosts (Rizzoli *et al*., 2009; Ruiz-Fons *et al*., 2012; Medlock *et al*., 2013). Elevated tick numbers in Great Britain have been attributed to an increase in the deer and red grouse (*Lagopus lagopus scoticus*) populations (Scharlemann *et al*., 2008). In northern Italy a change in land management has resulted in improved habitat suitability for small mammals and roe deer, important hosts for ticks. This has led to an increase in the incidence of tick-borne encephalitis (Rizzoli *et al*., 2009). This raises the important point that vegetation structure not only affects tick survival by manipulating microclimate, but also influences host availability. Grazers support fewer adult ticks than browsers and intermediate feeders (Gallivan and Horak, 1997). Density dependent mortality affects the stages from larva to nymph and nymph to adult (Randolph, 1993).

Tick populations are naturally controlled by birds such as oxpeckers, ants, beetles as well as bacteria, entomopathogenic fungi and nematodes (Walker *et al.*, 2003; Samish *et al.*, 2004). Oxpeckers feed exclusively on ticks, but numbers have declined in areas traditionally used for commercial beef production in response to the application of acaricides (Hockey *et al*., 2005). In six days a single young red billed oxpecker eats between 1100 and 1549 larval, nymphal and adult ticks. Extrapolated to an adult bird, this amounts to approximately 12 500 larval or 98 fully engorged tick females (Bezuidenhout and Stutterheim, 1980). The absence of oxpeckers may therefore have a considerable influence on tick population dynamics (since they remove adult ticks prior to reproduction) and subsequent levels of infestation in large ungulates.

3.4 Influence of Vegetation Structure on Local Micro-Climate

Empirical data from experiments investigating primary production within savanna systems provides insight into the effects of vegetation structure on local micro-climate. Soil moisture is generally higher beneath the tree canopy than further away (Scholes, 2003; Archibald and Scholes, 2007) due to the interception of solar radiation by the tree canopy and reduced rate of evaporation from the soil and vegetation beneath the canopy (Scholes, 2003). This is a complex effect, however, and depends on the fraction of the energy budget provided by radiation, and the fraction provided by the circulation of hot, dry air (Scholes, 2003). If sufficient energy is provided by the circulation of warm, dry air beneath the canopy, evaporative demand will remain high even in the shade (Scholes and Walker, 1993; Scholes and Archer, 1997).

Tree canopies trap and concentrate rainfall into larger input units, mainly in the form of drip-lines and stem-flow (Scholes and Archer, 1997; Scholes, 1998; Scholes, 2003). This increases the infiltration of rainwater into the sub-canopy soil, particularly near the base of trees (Scholes and Archer, 1997) and contributes to the maintenance of a higher soil moisture regime beneath the canopy than out in the open. Stem-flow can provide a considerable influx of water.

Trees typically enhance the pools and fluxes of soil nutrients beneath their canopies (Scholes, 1993; Scholes and Archer, 1997) via several mechanisms. Canopies trap aerosol minerals dispersed during the dry season, which are then washed into the sub-canopy soil during subsequent rainfall events (Scholes and Archer, 1997). There is evidence, albeit circumstantial, that trees act as nutrient “pumps”, drawing nutrients from the entire root zone (horizontal and at depth) and depositing them as litter at the soil surface beneath the canopy via leaf senescence (Scholes, 1993; Scholes and Walker, 1993; Scholes and Archer, 1997). A third mechanism is through trees serving as focal points for roosting birds and mammals seeking shade, cover or forage, and their subsequent faecal and urine deposits (Scholes and Archer, 1997). Leguminous trees fix nitrogen (Scholes, 1998). The consequence of elevated nutrient levels is stimulated herbaceous primary production resulting in a taller sward, denser cover and a more sheltered, benign environment for tick survival. The higher primary productivity may also attract hosts.

Tree crowns disrupt wind flow (Archibald *et al.*, 2009). In areas where tree cover is high enough, this serves to create eddies and push the wind above the tree crowns creating a sheltered sub-canopy environment. The sub-canopy is likely to maintain a higher relative humidity (RH), and hence more benign conditions for tick survival.

3.5 The Impacts of Ticks on Large Herbivore Hosts

Ticks have a range of detrimental impacts on their hosts. High tick infestations may cause anaemia, reducing production and threatening the health of young, old and sick animals. Up to 2500 larvae and nymphs may attach to each leg, 10 000 in all per animal (Bothma 1993). Control of ticks in game, particularly non-water dependent species such as eland, is difficult. Animal production has been found to be detrimentally impacted in a number of studies (Johnston *et al.*, 1981; Horak *et al*., 1983b; Jonsson *et al.* 1998). Jonsson (2006) managed to quantify the loss in production, finding that each engorged female tick was responsible for the loss of 1.37 ± 0.25 g of body weight in cattle.

Young animals are particularly susceptible to production losses associated with tick infestation, with studies showing that a moderate tick load on a growing lamb, in this case impala, can cause a weight loss of up to 44kg per year (Mooring *et al*., 2004). Impala have evolved allogrooming behavior that allows them to counter tick infestations. Scholtz *et al.* (1991) found that weaning weight in dipped Hereford cattle was 29.5 kilograms greater than in undipped Hereford cattle. The effects of individual engorging ticks ranged from 8-8.9 g per tick.

Ticks with large mouth parts, such as the bont tick (*Amblyomma* spp) and bont-legged tick (*Rhipicephalus* spp) may cause physical damage to the skin, leading to industry losses for trophies and processed products (Bothma, 1993). The bite site may also serve as an entry point for secondary infections, leading to abscesses and progressively worsening wounds that ultimately threaten the health of the animal (Bothma 1993).

The indirect transmission of viral, protozoan and bacterial diseases may also occur (Bothma, 1993). This may threaten the game population itself (eland are susceptible to heart water) or may be transferred to nearby commercial beef herds (gallsickness, heart water, red water) (Wesonga *et al.*, 2001).

3.6 The Relationship Between Eland (*Tragelaphus oryx*) and Their Environment, and Potential Implications for Tick Infestation

Social Organisation

Eland are gregarious, forming larger herds during the wet season compared to the dry season (Rowe-Rowe, 1983). This has been associated with the formation of nursery herds, where several family units amalgamate while their calves are young (Skinner and Smithers, 1990). The assumption made is that smaller groups come into contact with a greater surface area of vegetation, and hence are more exposed to ticks than larger groups of animals. The animals in the center of a larger group, usually the young, may have a lower exposure than animals on the periphery simply because vegetation is trampled. It is therefore anticipated that eland should be more susceptible to tick infestation during the dry season when they are dispersed.

Calving

Eland exhibit seasonal calving, with calving peaks usually occurring when there is a greater availability of green forage (McNaughton, 1990; Pappas, 2002). Skinner *et al*., (1974) found that eland breed throughout the year, but with a peak calving period during the early summer months (August to October in summer rainfall areas). Underwood (1973) concurred with this, although the season may vary geographically according to climatic conditions that favour the production of high quality forage, and the feeding preferences of the local eland population. Calving is relevant given the impact tick infestations can have on smaller bodied animals in terms of lost productivity. During the calving period herds may seek to minimize the exposure of young animals to the tick challenge by gathering into herds, or avoiding areas with high tick numbers.

Activity

The peak activity period of eland tends to be crepuscular and they utilize shade during the day (Pappas, 2002). Skinner and Smithers (1990) note, however, that they may feed into the

night during the summer months. Animals are likely to use woodlands for shade. They also move into wooded areas to escape wind and shelter from rain. Likewise eland move into open areas to regulate their temperature during cooler periods (Kerr *et al*., 1970). This behavior in response to temporarily unfavourable environmental conditions may bring eland into contact with areas of high tick abundance, increasing their risk of becoming infested.

Food

The stomach morphology and structure of eland are more closely associated with that of browsers, suggesting that they are unable to digest mature grass as well as grazers (Watson & Owen-Smith, 2000). Their diet is usually restricted to greener, newly-sprouted grass (Hofmann, 1973; Owen-Smith, 1982). Using a different approach, Sponheimer *et al.* (2003) examined the dietary composition of several bovids through the analyses of stable carbon isotopes from teeth enamel, bone collagen and hair samples. The results indicate that, although eland may include grass in their diet, in the sampled populations it is a minor constituent (about 10% of their diet). Codron *et al*. (2006) analyzed C3:C4 ratios and nitrogen percentages in faeces sampled at sites in the Waterberg region of Limpopo Province. Eland were concluded to have a strongly C3-based diet, so they were considered almost strictly browsers confirming the current evidence for southern African populations. Similarly Wallington *et al.* (2007) analysed faecal stable carbon isotope ratios in Suikersborand Nature Reserve in Gauteng and found that C3 plants (browse) formed 95% of eland diet in March (late wet season) and June (early dry season). They suggest that eland populations in savannah environments exhibit a larger browse percentage in their diet than populations living in grasslands. Hence the overwhelming consensus is that eland are mainly browsers (McNaughton and Georgiadis, 1986; Buys 1990; Watson & Owen-Smith, 2000) or mixed-feeders, but the extent to which they graze remains uncertain. In southern Africa they are assumed to be browsers during the dry season, and grazers only during the new growth flush following the onset of spring rains (Buys, 1990; Fabricius & Mentis, 1990; Watson & Owen-Smith, 2000; D'Ammando *et al.,* 2014, citing Kerr, Wilson & Roth, 1970). Kerr *et al.* (1970) found that in Zimbabwe eland spent approximately 85% of the time browsing, 10% of the time feeding on forbs and 6%-7% of the time grazing.

In contrast, research from Tanzania (Lamprey, 1963), Limpopo (Hofmeyr, 1970) and the Drakensberg region of South Africa (Rowe-Rowe, 1983) indicates considerably more utilization

of grass, although this is likely to be seasonal. Buys (1990) reported that feeding on woody plants increased from 25% in the wet season to 65% in the dry season in Mpumalanga, South Africa, while forbs were noted as an important component of the diet. A more recent study in the Magaliesberg region of South Africa found that grasses constituted 31.8% of the plant species eaten during the dry season winter months (D'Ammando *et al*., 2014). Contradicting the findings of Buys (1990), D'Ammando *et al*. (2014) found that forbs were generally avoided, and that most of the browse component of the eland diet consisted of woody species. Most of the grazing was also limited to a single species, *Tristachya leucothrix*. In view of the above variation in findings, it has been suggested that diet composition may vary between different eland populations in different geographical regions, and under different management conditions.

Eland have a high metabolic rate, and require a diet with high protein content (Pappas, 2002). Owen-Smith (1987) used a model to predict that eland should prefer vegetation types with an abundance of browse species with a high leaf:stem ratio to meet the high protein requirements. The types identified were forb rich grasslands/ savannahs or broad-leafed savannahs. The significance of this is that the quest to maximize the quality of their diet is likely to be a major determinant of eland movement patterns, which may or may not bring them into contact with ticks. According to the theory that an organism satisfies a hierarchy of needs sequentially in order of temporal importance, then any influence that tick abundance exerts on eland movement is likely to be related to the quality of forage available at that time. When forage quality is limiting, eland may prioritise maximizing their diet and exploit the available resources to this end irrespective of tick abundance. Under conditions where forage quality is easily maximized, eland may be in a position to prioritise minimizing tick infestation, and accordingly alter their movement patterns.

A further consideration is the influence of the management area on the patterns of resource use by eland. Under what may be considered natural conditions, such as those in large protected areas, free roaming eland herds have been found to have a home range of up to 500 km^2 (Skinner & Smithers, 1990). Many of the studies on eland have been undertaken on properties far smaller than this (Kgaswane Mountain Reserve, for example, is approximately 50 km^2 in area). It is possible that physical or behavioural confinement forces eland to shift from being large, roaming concentrate selectors to periodic facultative grazers. Eland are not dependent on water, obtaining their water requirements from their diet (Bothma, 1993; Skinner and Smithers, 1990).

Contribution to the Game Industry

Eland contribute to the game farming industry through trophy hunting, as the biggest and most easily accessible African bovid (Estes, 1999). They are a sought-after component of a discerning trophy collection, with a current approximate cost of R26 420 per trophy (www.africanskyhunting.co.za). In addition, they contribute to ecotourism, being gregarious and sometimes forming large herds (Jarman, 1974; Estes, 1999). They produce hides similar in size to cattle, and carcasses dress out at 235-464kg (Bothma 1993), similar in mass to a buffalo. The meat is also of good quality (Skinner and Smithers, 1990). Eland therefore have a part to play in the industry. Live sales reached R5 473 to R7 153 per animal in 2012 (Farmers weekly, 2013), with a record price of R205 000.

My study may be viewed at two scales, the first being as applied specifically to eland. The outcomes may therefore be of practical relevance to landowners who have eland within their properties. At a broader level, eland may also be used as a surrogate for any kind of large wild ungulate and it may be possible to extrapolate the results of the study to managing the populations of a wider variety of animals in small game reserves and on game farms.

4. HYPOTHESES

Hypothesis related to objective 1:

1.1 The areas consisting of tall, stemmy grasses interspersed with low shrubs will contain the highest numbers of ticks. The short, mesic grasslands on the ridges will contain the lowest tick numbers.

Hypotheses related to objective 2:

In view of the literature indicating that tick larvae mortality is positively correlated to lower relative humidity, it is expected that adult ticks are better suited to withstand drier conditions than immature ticks. Hence the hypotheses are:

2.1 That adult ticks will be more prominent during the early wet season (November), and the larval and nymph stages dominate the wetter months towards the end of summer (February); and

2.2 That adult ticks will be located in higher proportions in the more sheltered structure types since the higher temperatures and lower relative humidity likely to occur in the more open vegetation structure types causes high mortality among smaller moulting ticks. Hence fewer ticks reach maturity in these areas.

Hypotheses related to objective 3:

3.1 The temporal patterns of diurnal tick activity correspond with that of eland, since this is likely to increase the chance of intersection with a host. I expect the diurnal temperatures to be higher in February than in November, with the warmest period over midday constituting a higher proportion of the day. Hence, more ticks will be intercepted in the morning and later afternoon than during the heat of the midday period; and

3.2 This pattern will be more pronounced in February than it is in November.

Hypothesis related to objective 4:

4.1 Eland will minimize their calves' exposure to areas of high tick abundance by either avoiding areas with high tick densities, or moving rapidly through them.

5. CRITICAL QUESTIONS

The hypotheses have been condensed into the following critical questions asked during the study. The questions seek to guide the collection and analysis of the data.

Objective 1:

1.1 Is there a relationship between vegetation structure and tick abundance?

1.2 If so, what is the strength of this relationship across vegetation structure types?

1.3 What is statistical significance of any existing relationship?

Objective 2:

2.1 How are the tick developmental stages distributed across the respective vegetation structure types?

2.2 Is the distribution of age classes statistically significant between the vegetation structure types?

2.3 Is there a difference in the tick age class distributions between the two sampling periods?

Objective 3:

3.1 What are the temporal patterns of diurnal tick activity evident during the sampling periods?

3.2 Do these differ statistically between vegetation structure types?

3.3 Do they differ significantly between sampling periods?

Objective 4:

4.1 Do eland avoid areas with high tick abundance and select areas with low tick abundance?

4.2 If so, is there a change in this behavior between the two sampling periods?

6. MATERIALS AND METHODS

6.1 Study Area: Kgaswane Mountain Reserve

KMR is situated on the outskirts of Rustenburg in the North West Province of South Africa (25^{o} 43' S, 27^{o} 11' E) (Figure 1). The reserve encompasses a range of interlinking environmental gradients (eg. soil type; vegetation composition; forage quality; temperature;

humidity; aspect; altitude; precipitation), each of which are likely to influence the biotic and abiotic determinants of tick abundance.

Altitude and Climate

There is an altitudinal gradient associated with a drop in height from 1660m above sea level (a.s.l) at the top of the Magaliesberg in the western half of the reserve to approximately 1200m a.s.l at the floor of the valley system in the eastern part of the reserve (Nel, 2000, citing Coetzee, 1975; Parrini and Owen-Smith, 2010). The mean long-term annual rainfall is approximately 687mm ± 208.4mm (Nel, 2000), with the high variability typical of semi-arid regions (Scholes and Walker, 1993; Scholes, 1998). Rainfall is highly seasonal, with 88% of the MAP falling between October and March (Parrini and Owen-Smith, 2010). Although the regional climate is constant, the topography establishes the following local environmental gradients:

Temperature: Cooler in the uplands, warmer in the valleys, particularly during the summer months. Uplands are subject to cooling breezes during summer. Valley bottoms have cooler night-time temperatures in winter, but winter frosts in the uplands are likely to be more frequent.

Moisture: Uplands are a net exporter of rainfall via surface runoff (a function of topography) and subsurface seepage through the coarse, shallow soils. There are greater evaporative losses from the more exposed landscape, and greater evapotranspiration losses from the shallower soils. The lower lying areas are net sinks of moisture due to the accumulation of runoff. The deeper soils in the valley bottoms encourage the dominance of trees and shrubs, the shade of which reduces evaporation demand on the soil. The deeper soils also have greater storativity of soil water.

The environment in the bottomlands is likely to be moister, which translates into a different vegetation community and a different vegetation structure. This is likely to influence parameters such as local temperature; relative humidity; incidence of frost; and fuel loads and hence fire frequency and intensity, which may in turn affect tick abundance.

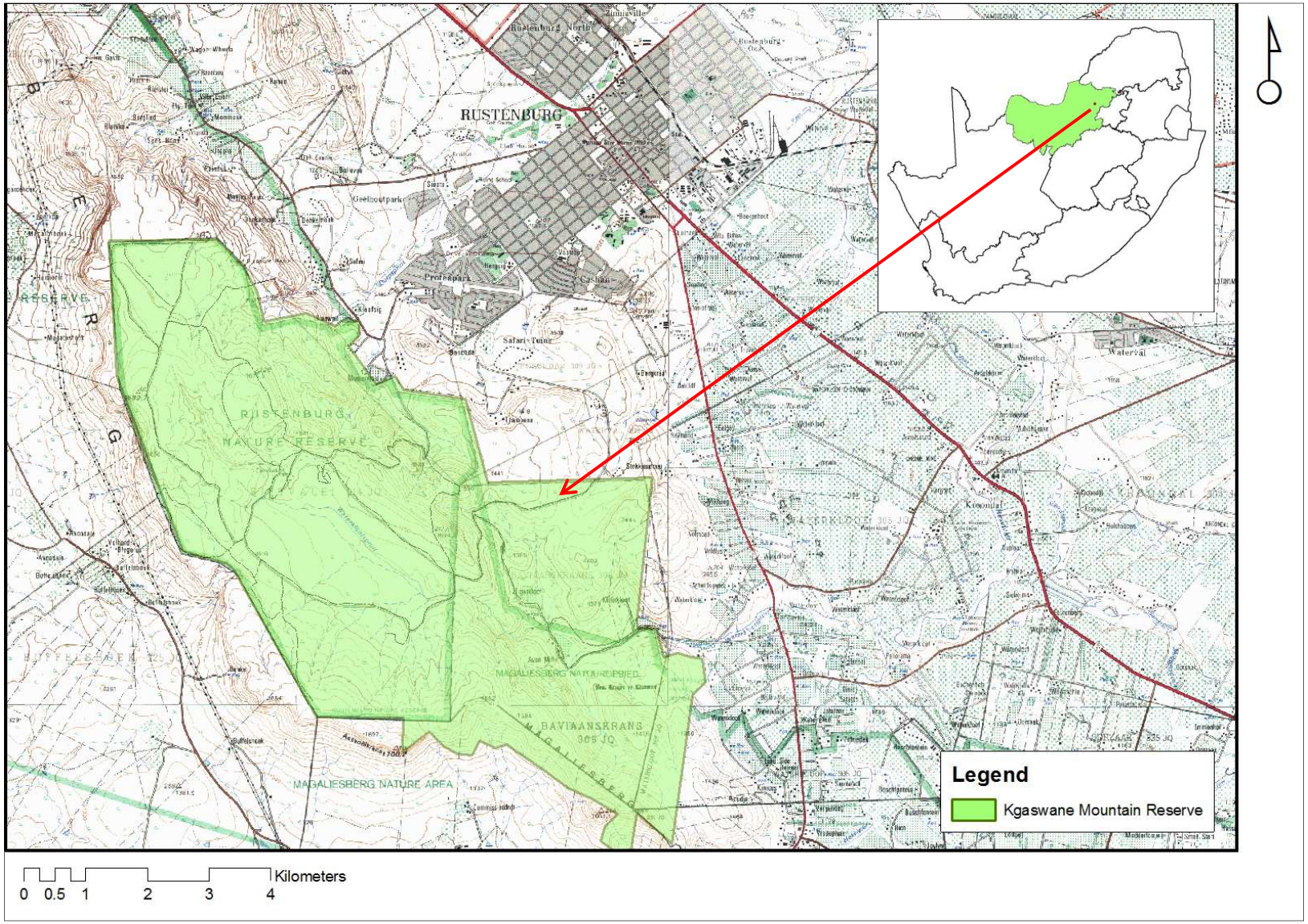


Figure 1: The Study Site: Kgaswane Mountain Reserve, south of Rustenburg on the eastern periphery of the North-West Province, South Africa (indicated in the inset).

Geology and Soils

The reserve is predominantly underlain by two geological formations, namely the recrystallised quartzite of the Transvaal System and the norite intrusions of the Bushveld Igneous Complex (Nel, 2000). The high-lying summit and slopes are underlain by relatively homogenous beds of coarse-grained quartzite and minor hornfels (Coetzee, 1975). The lower-lying, valley bottom regions are dominated by Kolobeng Norite, a base-rich, fine-grained igneous mineral (Figure 2).

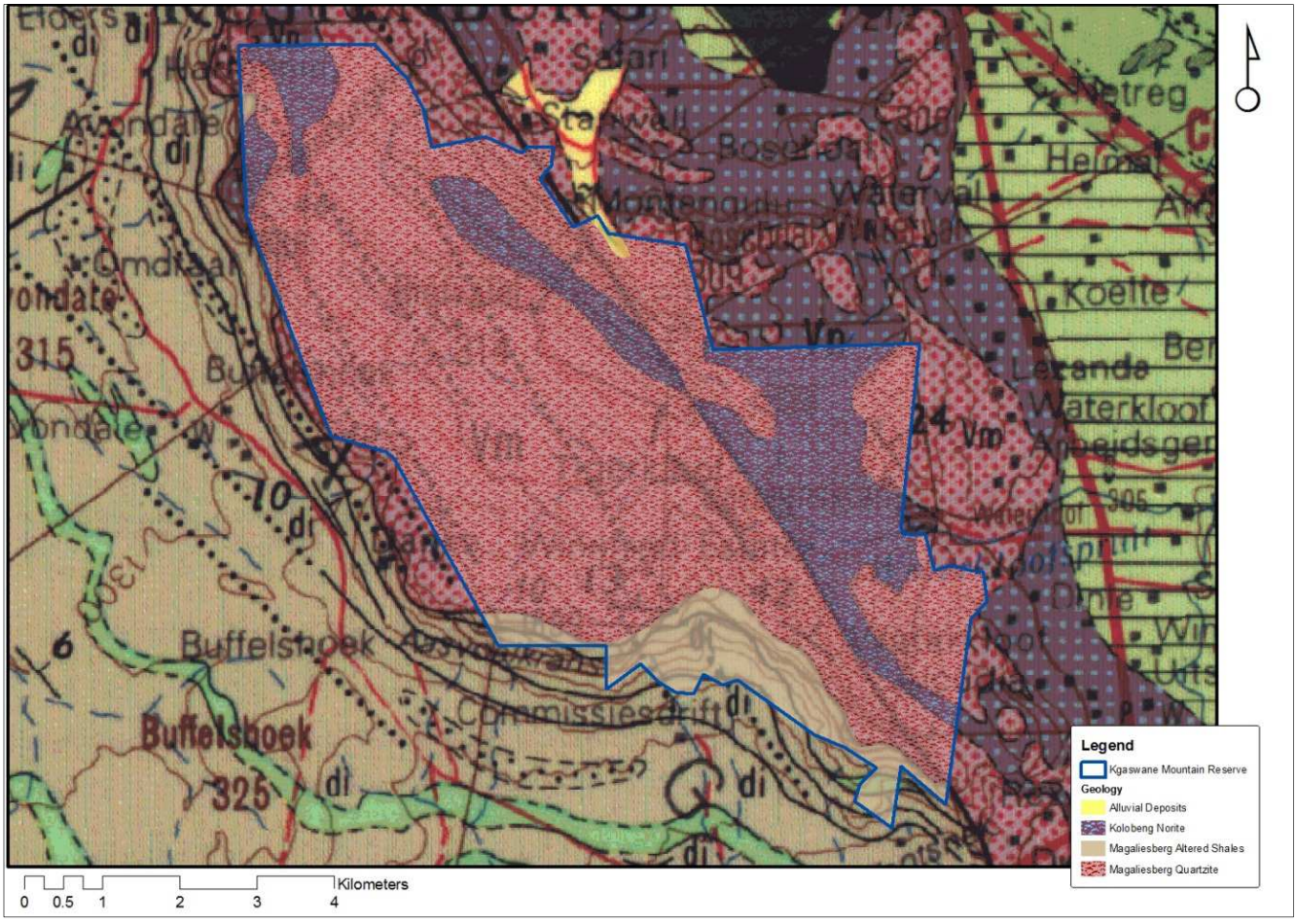


Figure 2: The geology of the Kgaswane Mountain Reserve

The significance of geology is the influence it has had on local soil formation. Pedogenesis is driven by the integrated influences of parent material, topography, climate, time and organism activity (Fey, 2010). The combination of these factors within the study site has

resulted in a spatial soil distribution characterised by shallow, sandy soils in the uplands and on the steep slopes overlooking the valley bottoms (Nel, 2000). These are approximately 15cm deep Mispah (orthic A/ hard rock) loamy sands (Soil Classification Working Group, 1991). The soils in the footslope regions are deeper and more clay-rich. These are mostly Glenrosa (orthic A/ lithocutanic B) soils up to 25 cm deep. Colluvial deposition at the base of the slope is a dominant pedogenic process, establishing a soil environmental gradient. Relatively deep, loamy, well-drained and nutrient-rich soils characterize the valley bottom soils. Hutton (orthic A/ red apedal B) is the dominant soil form with depths ranging from 30 to 40cm (Nel, 2000).

Vegetation

Nel (2000) identified four major vegetation groups, namely:

a) Vegetation associated with shallow soils and bedrock, underlain by quartz. These characterize the steep northern and central ridges;
b) Vegetation associated with deep to medium-deep, well-drained soils, also underlain by quartz. These dominate the central basin and north western plateau of the reserve;
c) Vegetation associated with deep clay-dominated soils underlain by diabase, mostly confined to the eastern valleys; and
d) Vegetation associated with moist habitats and riparian drainage lines.

These were described and mapped according to their association with the dominant substrate types. This was further refined into 51 vegetation communities based on a combination of the composition of the dominant species and the structure of the woody and herbaceous vegetation (Nel, 2000). Vegetation structure is defined as the organization of space of the individuals that form a stand (and by extension a vegetation type or a plant association) (Edwards, 1983 citing Dansereau, 1957). The primary elements of structure are growth-form, vertical stratification and coverage (Edwards, 1983). Nel (2000) has grouped the vegetation types according to the variable quadrant size method described by Coetzee and Gertenbach (1977). The vegetation classes created are similar to those outlined in Edwards (1983), which provides a practical, robust and broad-scale classification system for the structure of vegetation. The system

is hierarchical, and based on the dominant primary growth form types, cover, height and, to a lesser extent, substrata. The primary attributes used are:

- A primary set of four growth form types (trees, shrubs, grasses and herbs);
- A primary set of four cover classes (closed, open, sparse, scattered) for each growth form type;
- A set of four height classes for each growth form type (high, tall, short, low).

The resulting permutations yielded 72 potential vegetation structural groups (refer to Edwards, 1983).

Nel (2000), in his vegetation classification, identified and mapped 13 structural groups across the 51 vegetation communities. The structural classification is independent of species composition, although this information is provided. My study is more concerned with vegetation structure than species composition, and seeks to establish the main vegetation structural gradients across the study area.

6.2 Research Design

Vegetation Structural Types

The establishment of vegetation structure types for the study was based on the existing vegetation map from Nel (2000) and the associated data obtained from the North West Parks and Tourism Board (NWPTB). Nel (2000) divided the various distinct vegetation types into thirteen vegetation structural units. Ideally, tick abundance would have been sampled for all thirteen types. This may have yielded a more sensitive, robust and certainly more comprehensive dataset with the added advantage of spatial consistency across studies. However, the time-frame available for my study precluded the sampling of all thirteen units, and this number was refined by simplifying the classification criteria.

A key assumption of this study is that tick abundance will vary according to the relative humidity and temperature within the herbaceous vegetation layer. The main structural determinants of these variables are assumed to be the height of the grass layer; the height of the tree layer; and the density of the tree layer. At a broader level, and according to visual

assessment, the vegetation types within the reserve were divided into the groups as described in Table 1.

The vegetation structure types were mapped in ArcGis 9 (Environmental Systems Research Institute (ESRI), Redlands, CA, USA), using the vegetation-type shapefile from NWPTB as a foundation. This was overlain on georeferenced 2012 black-and-white aerial imagery, obtained from the Surveyor Generals Office at Mowbray. Google Earth™ satellite imagery was also used as a reference. The mapped polygons were modified and merged according to the dominant structural unit. Mapping was done at a scale of 1:5 000. The polygons were then ground-truthed to ensure that the map appropriately represented the vegetation structure seen on the ground.

It should be noted that certain areas of the Tall Lowland Grassland (TLG) are artificial due to the influence of human activities. The construction of earthen dam walls across the main valley bottom has resulted in the subsequent mobilization and deposition of sediment, which has modified the species composition of the sward. The impoundments across the valley are also retaining much of the longitudinal flow, resulting in a change from a sward dominated by *Hyparrhenia hirta* and *Hyperthelia dissoluta* to one dominated by *Imperata cylindrica*, a shorter, hygrophilous species. The maintenance of a servitude beneath a power-line is maintaining an artificial grassland adjacent to the valley bottom riparian zone by routinely removing trees that reach a certain height. In these areas, the over-riding consideration was the structure of the vegetation. Hence modified areas were included in the overall classification of the TLG structure type even though they may have occurred in an atypical position in the landscape.

Thicket and genuine stratified forest areas are also present within the reserve. They are, however, thinly distributed and spatially limited. Within the context of the reserve and their expected contribution to eland resource use, they are assumed to be relatively unimportant. The density of the tree layer, and the dearth of a grass understory, requires a different sampling strategy as drag cloths proved to be impractical. The decision was taken to include these structural types in the Tall Closed Woodland (TCW) group, based on the additional assumption that they would fulfil a similar ecological role in relation to eland use.

Tick Data

Data were collected over two sampling periods, namely November 2014 and February 2015. According to long-term rainfall data (www.accuweather.com), the wet season in Rustenburg usually begins in October and ends in April, with peak precipitation occurring in November and January (Figure 3). The rainfall pattern for the 2014/2015 season appears to broadly conform to this trend (Figure 3).

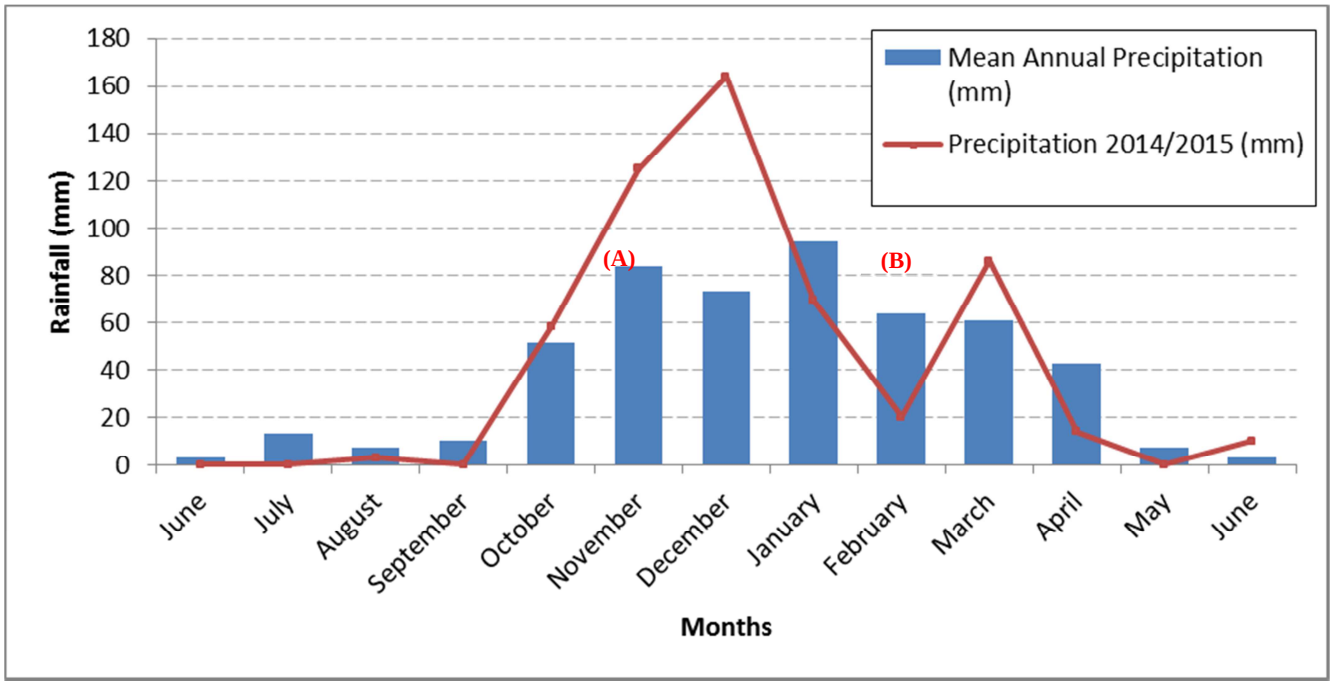


Figure 3: Mean Annual Precipitation (MAP) data for Rustenburg (www.accuweather.com/en/za/rustenburg; www.worldweatheronline.com/ Rustenburg-weather-averages/North-West). The bars represent the average precipitation per month, while the line represents rainfall data recorded from June 2014 to June 2015. Point (A) represents the first sampling period, and (B) represents the second sampling period.

However, analysis of the individual rainfall event data reveals that in October 2014 a single rainfall event on the 25th accounted for 80% of the monthly total (www.worldweatheronline.com/Rustenburg-weather-averages/North-West). In addition, 85% of the rainfall in November 2014 occurred in the last week of the month, with regular rainfall

events for the following two months. The major rainfall event at the end of October undoubtedly initiated the critical vegetative phenological processes, visually signaling the onset of the wet season. However, given the prevailing high evaporative demand; the desiccated soil profiles and the dry month-long period immediately following the storm event, I reasoned that the environmental conditions that affect tick larval and nymph mortality may not have been sufficiently influenced by that single rainfall event. I assumed that, from a ticks eye view, the wet season began once rainfall occurred at intervals sufficient to maintain soil and lower vegetation/ litter-strata moisture levels, in so doing perpetuating the environmental conditions that influence wet-season tick mortality. The wet season in 2014 therefore essentially began *properly* on the 23rd November (www.worldweatheronline.com/Rustenburg-weather-averages/North-West).

November 2014 and December 2014 were notable for the higher than average rainfall that occurred (Figure 3). December was remarkably wet, receiving approximately double its long-term average precipitation. January 2015 and February 2015 were drier than usual, with February markedly so in receiving half the expected precipitation (Figure 3). The rainfall data during March 2015 were also skewed by a single event where 67mm of the total of 86mm fell (www.worldweatheronline.com/Rustenburg-weather-averages/North-West).

The study site is situated in a semi-arid savanna region with a rainfall regime characterized by its variability (Scholes, 1998; Uys, 2006). Within the temporal context of the study, the bulk of the annual precipitation fell between the last week of November and the end of February, with the periods of the wet season on either side characterised by unseasonably dry conditions punctuated by single rainfall events. The sampling periods occurred during November 2014, extending into a wet period, and the first two weeks of February 2015 where little rainfall was encountered. It is hence fair to say that the first sampling period corresponded with early summer prior to the onset of the wet season, and the second sampling period corresponded with late summer following the culmination of the wet season. This is particularly so in view of the unusually dry February and early March.

The reserve was mapped according to the seven structural units, and three representative sites (Sites A, B and C) were selected within each unit. The structural unit represents the population, or entire vegetation structure class, being studied. Each site represents a sample, and there are hence three replications per structural unit (Figure 4). Within each site block, 3 drags were carried out, moving in a zig-zag fashion across the block. Spickett *et al.* (1992) and Zeiger

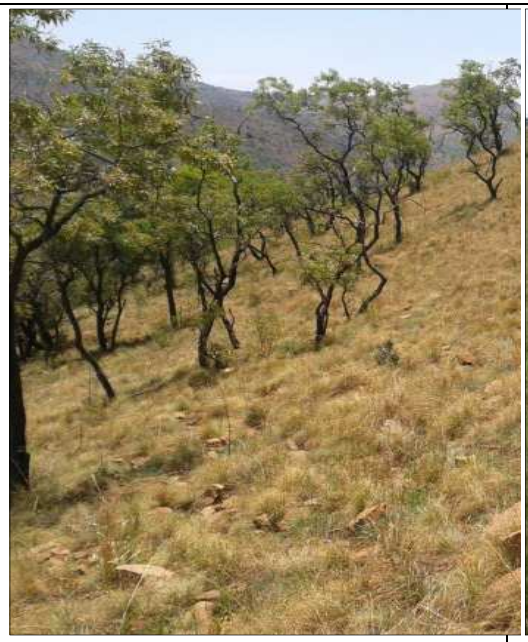
et al. (1998) used a length of 250 m per drag, Daniels *et al.* (2000) used a 60 m by 60 m grid while Ruiz-Fons *et al.* (2013) used a 100 m drag transect. A potential problem highlighted is that ticks are not only picked up by the flannel, but are also brushed off by the vegetation. It was decided to adopt a transect length of 50 m as the sampling unit to allow more samples to be taken within the time allotted. Three 50 m drag transects were carried out within each block at each site, representing 3 samples per site.

Ecological research aims to maximize the amount of information contained in the data collected. The samples collected were distributed temporally across the day to account for any confounding influences due to the weather, and to investigate these. Within each block at each site, one drag was performed in the morning (07h00 to 10h00); one drag during the middle of the day (11h00 to 15h00); and one in the afternoon (15h00 to 18h30). There were hence nine samples taken from each temporal period within each structural unit, and twenty-seven samples were taken from each structural unit during a sampling period. A total of 189 samples were taken during each sampling period, and the total number of drags for this study was 379.

Table 1: Vegetation Structural Types Identified within KMR.

Vegetation Structure Unit	Description	Photo: Sampling Period 1	Photo: Sampling Period 2
1. *Short upland grassland*	• Trees are largely absent; • Bulk of the sward is less than 30cm in height; • Vegetation is characterized by granitic rock at the surface, and shallow coarse soils; • Shrubs are prominent, but generally the same height as the sward and too sparsely distributed to affect microclimate; • Seasonal variation in structure is associated with the culms of *Themeda triandra* and *Loudetia simplex*.		
2. *Tall Upland Grassland*	• Trees are absent; • The bulk of the sward volume is greater than 40cm in height; Occupies the mid-slope and foot-slope areas of the topography; • Characterized by deeper, sandy clay soils; • Termitaria are prominent.		

3. *Tall Lowland Grassland*	• Situated in the valley bottoms in the lowest parts of the reserve; • Characterised by a flat topography, fairly deep clay soils and dense, tall herbaceous vegetation with *Hyperthelia dissoluta* and *Trachypogon spicatus* dominant species; • Trees and shrubs sparsely scattered and unlikely to influence the microclimate; • Bulk of the sward approximately 70cm in height, flowering culms raise this to in excess of 1.2m;		
4. *Tall Open Woodland; Tall Grass Layer*	• Generally occupies the mid-slope areas in the eastern part of the reserve; • Tree layer is generally 3m to 5m in height and sparsely distributed; • Tree density is, however, judged to be sufficiently dense to a) influence grass species composition (and therefore structure); and b) influence wind movement and hence microclimate. • The dominant tree species are *Faurea saligna* and *Acacia caffra*. • The grass component is similar in height and species composition to the Tall Lowland Grassland.		

5. *Tall Open Woodland; Short Grass Layer*	• Occupies the upland areas on the eastern side of the reserve; • Characterized by a scattered tree layer of 3m to 5m in height and a dense short sward, the bulk of which is approximately 30cm in height; • The dominant tree species are *Faurea saligna* and *Protea caffra;* • The grass sward tends to be dominated by typical mesic short grassland species such *as Themeda triandra, Heteropogon contortis, Panicum coloratum, Loudetia simplex,* and *Tristachya leucothrix.*	 
6. *Shrubland; Tall Grass layer*	• Occupies an area at the head of the main valley in the reserve; • Characterised by a prominent, moderately dense layer of trees less than 2 m in height, with *Rhus rehmanniana* and *Maytenus heterophylla* dominants; • The grass layer is tall (>1.5m in height), dense and dominated *by Hyparrhenia dregeana* and *Hyperthelia dissoluta.*	 

7. *Tall Closed Woodland*	• Characterised by a dominant tree component whose canopies overlap; • Tree height is generally >5m; • The grass layer is short and relatively sparse; • Includes thicket and forest structures.		

Structural Group 1: for example Tall Upland Grassland

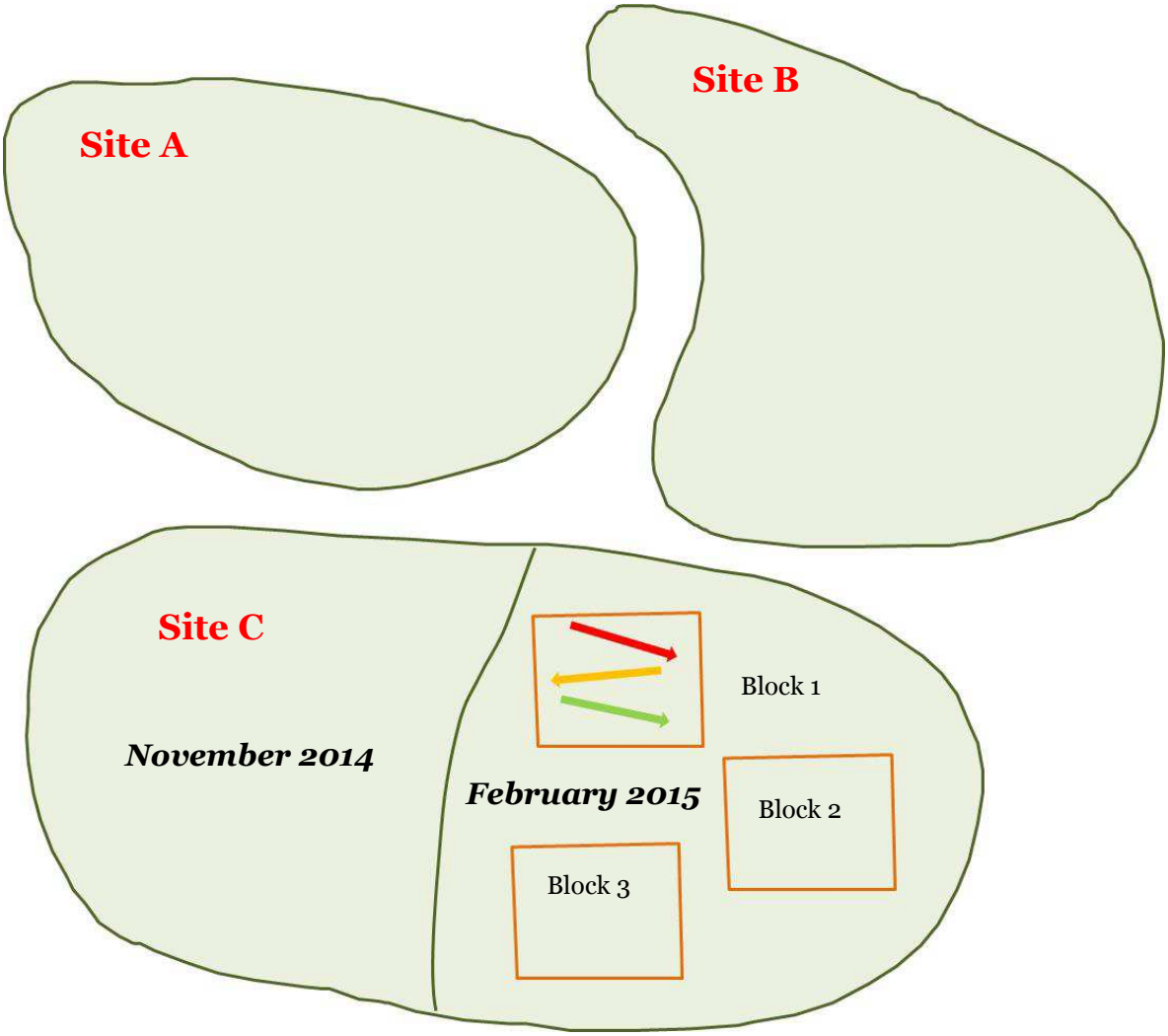


Figure 4: Experimental design. Three representative sites are chosen from each vegetation structural unit. Each site is divided into two sampling periods, which is in turn divided into three sampling blocks. Within each sampling block, one drag is carried out in the morning (red arrow); midday (orange arrow) and afternoon (green arrow).

Care was taken in selecting the blocks, to ensure that the area being sampled was as homogenous as possible. The blocks were positioned perpendicular to the contour, ensuring that transects included the gradient, and that the environmental influence was distributed evenly across all blocks and transects. The confounding influence of environmental gradients was

minimized at each site. Each site was flat and approximately 300 m x 400 m in dimension, the intention being to divide each site into two blocks of approximately 150 m x 200 m to enable "fresh" vegetation to be sampled during each data collecting iteration (Figure 5). The sites and blocks were selected and marked using a GPS.

Eland Data

One eland cow was fitted in 2012 with a Global Positioning System (GPS) collar (Africa Wildlife Tracking, http://www.awt.co.za) that allowed GPS locations to be recorded (Plate 1). Collars were fitted to three additional eland cows in September 2014. Location data in the form of GPS coordinates at 4-hourly intervals were obtained for the duration of the study period. These data were used to determine the location of the eland in relation to the defined vegetation structure types.

Plate 1: Eland cow with GPS collar.

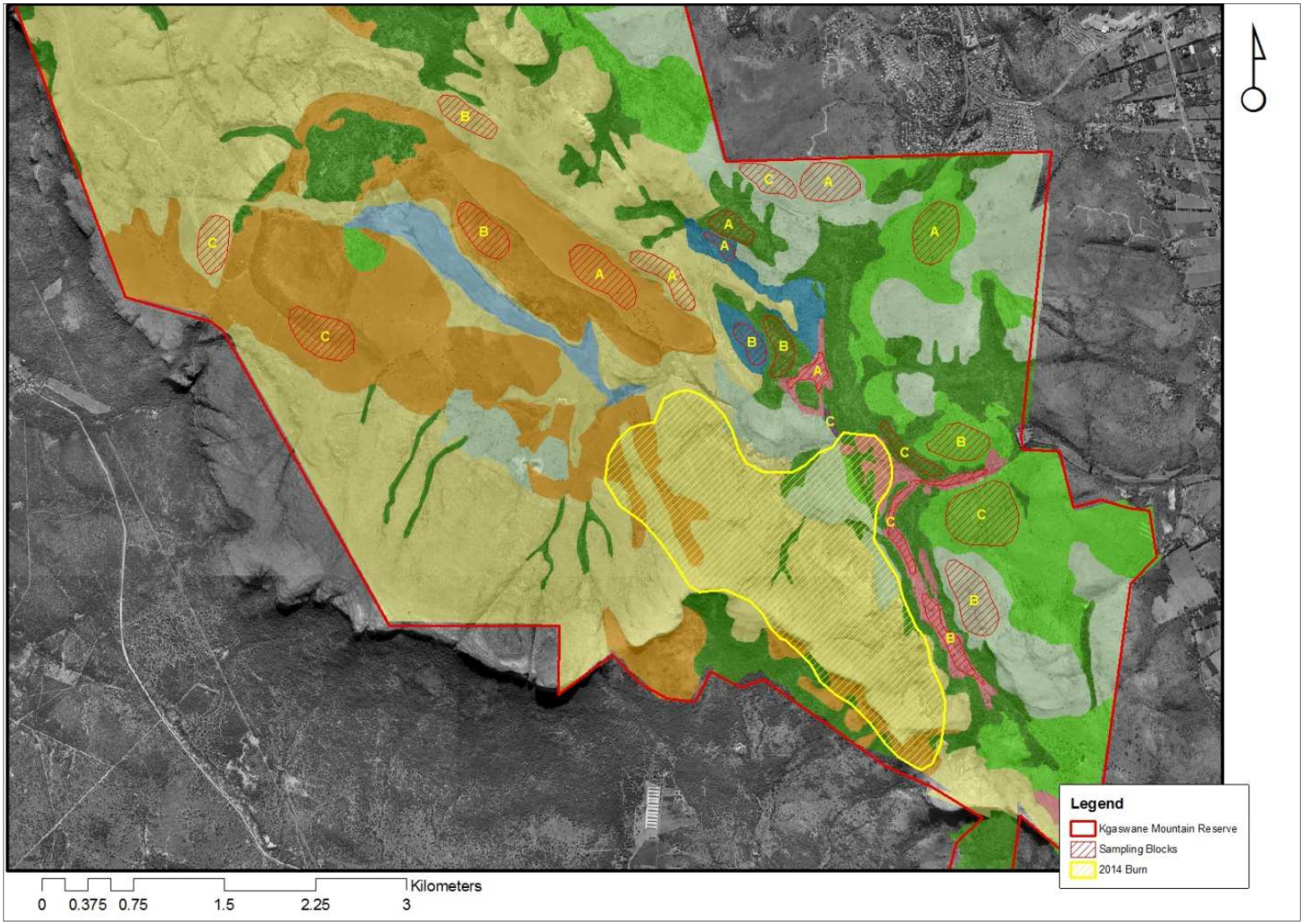


Figure 5: Experimental design: Position of the three sampling blocks (A, B and C) for each vegetation structural type. The area marked in yellow cross-hatching is the approximate position of a burn applied shortly before sampling commenced in November 2014. This area was avoided.

The data captured by the GPS were transmitted via satellite to a secured database that was accessible through the internet. The original intention was to download the location data for two periods, namely November 2014 and January 2015, to coincide with the sampling periods. However, a large portion of the area frequented by the first collared eland cow was burned prior to the November sampling period, resulting in a flush of newly-sprouted green grass cover. The provision of high-quality forage attracted the eland onto the burned areas, introducing a confounding factor to the movement data during this period. To counteract this, the assumption was made that the patterns of tick abundance within each vegetation type are likely to be similar from year to year, since the hypothesis being tested is that eland are able to link tick abundance with vegetation structure at certain times of the year, and alter their movements accordingly. Eland movement data for the sampling periods (November 2014 and February 2015) were downloaded and compared against tick abundance across the vegetation structure types. In order to account for the potential distortion in animal behaviour introduced by the burned area, the current results were compared to movement data from the same periods of the preceding year. In the event of a substantial difference in movement patterns, the data from the preceding year would be used as a surrogate for the current season, particularly since it is known that no parts of the collared eland's home range were burned during the previous year.

It should be noted that the effect of the fire on forage palatability was assumed to have waned sufficiently by the second sampling period for an influence on animal movement to be unlikely. Fires remove cured grass biomass, exposing the grass growing tips to light and stimulating the production of new shoots (Tainton, 1999). These are usually considered highly palatable (O'Connor *et al*., 2010). Over the course of the subsequent growing season the lignin content of the new grass growth increases, structurally enabling the leaves to be held in such a way that light capture is maximized within a competitive environment (Tainton, 1999). The consequent reduction in the carbon to nitrogen ratio within the leaf material has a negative impact on crude protein content, resulting in a reduction in perceived palatability by animals (Tainton, 1999). Certain grass genera, most notably *Cymbopogon* and *Elionurus*, produce phenols and turpenoids that act as grazing deterrents (Van Oudtshoorn, 1992; Scholes, 1998; Tainton, 1999). These accumulate over the course of the growing season. It is fair to say that the quality of grass forage decreases as the proportion of lignin and turpenoids in the forage material increases, and the sward becomes collectively unpalatable to all but specialist grazers (Tainton, 1999). Facultative grazers and mixed feeders hence become increasingly more selective in their

grazing preferences as the growing season progresses. The attraction of animals to the burned area is likely to wane until it fails to influence animal movement patterns (Archibald *et al.*, 2005).

6.3 Data Collection

Within each 50 m transect, ticks questing on vegetation were collected by drag-sampling using a modified method described in detail by Spickett *et al.* (1992). This entails dragging a 1 m x 1 m piece of white flannel cloth along the transect. A drag sampling apparatus was designed using three wooden broomsticks and a series of crocodile clips (Plate 2).

Plate 2: The drag apparatus used in sampling.

The draw bar consisted of a wooden broom handle approximately 1.2 m long with four large crocodile clips attached equidistantly across its length. The apparatus was designed to aid the rapid and simple change of drag-cloths in the field. Another wooden broom handle was attached to the distal end of the drag-cloth with five smaller crocodile clips, the purpose being to weigh the cloth down and ensure that the cloth is kept in contact with the vegetation while dragging. The third wooden broom handle was attached to the drawbar by a nylon rope, and allowed me to drag the cloth away from my legs while walking, ensuring that all ticks encountered along the sampled transect were picked up by the cloth rather than my legs.

Each collection was made by pulling the spar a distance of 50 m. At the end of each transect the flannel cloth was removed from the bar and put into a labelled zip-lock bag. The ticks were removed with fine-point forceps, counted and placed in a tub containing 70% alcohol.

The parameters measured were: tick number; and developmental stage (adult, nymph and larva) based on size class. Ideally species identification to genus level would also have been recorded using Walker *et al.* (2003), the primary objective being to divide the ticks up into 1-host, 2-host and 3-host ticks and identify and compare their patterns of abundance. However, not having an entomology background, the time taken to do this reliably would have strained the project schedule. While this is certainly valuable data to have, it was deemed surplus to the information required to meet the objectives of the study.

Care was taken to drag-sample areas where tick numbers had not been influenced by previous sampling. Drags were not carried out over dew-laden grass early in the morning, or after rain, as wet flannel decreases its efficacy. Data collection was carried out over three diurnal time-periods, namely morning (7 or 8 am to 11am), midday (11am to 3pm) and afternoon (3pm to 6:30pm). Each site was sampled once at each time period during each of the sampling iterations. The identification of seven vegetation functional types, with three replicate sites and three blocks within each site (and using the individual drag as the sampling unit), equated to 189 drags being made during each sampling period.

ESRI ArcGIS 9 was used to determine the area and proportion as a percentage of the area of the nature reserve of each of the vegetation structure units. The same software was used to overlay the eland GPS positions on the map and to calculate the number of eland observations per structure type. GPS data were downloaded for the current sample periods, namely early November 2014 and late January 2015. Data were also downloaded for the same periods of the previous year (early November 2013 and late January 2014) to compare and account for any possible distortion to eland movement caused by the late season burn in 2014.

6.4 Data Analysis

Tick Abundance and Vegetation Structure

Although the sampling sites were strategically placed across the landscape to ensure environmental homogeneity and reduce the risk of variance introduced to the data by environmental factors, the blocks and drags were essentially randomly scattered across the sites. At the landscape level it was assumed that ticks are uniformly distributed within each structure type. Although it was assumed that the macro-environmental conditions are uniform across the

structure blocks, realistically it is impossible to quantitatively determine the full array of variables that govern tick distribution since so much of it is dependent on the random occurrence of hosts. Hence, intuitively, the data are likely to be non-parametric i.e. they are not normally distributed. To confirm whether the data are non-parametric, Shapiro-Wilk W tests were performed (Steel and Torrie, 1980). The null hypothesis to be tested is that the data are normally distributed. If W is significant, then the hypothesis that the data are normal should be rejected. The closer W is to 1, the more normally distributed the data.

For normally distributed data a 1-way analysis of variance would be most appropriate for determining statistically whether abundance varies across vegetation structure types. The equivalent test for non-parametric data is the Kruskal-Wallis (KW) test, which uses ranked data rather than the actual data (Steel and Torrie, 1980). This was performed on the datasets from the two sampling periods, the null hypothesis being that the amount of variation explained by vegetation structure is not significantly different to zero.

Dunn's test is a post-hoc procedure for the KW test to make multiple non-parametric pairwise comparisons of tick abundance between the vegetation structure types (Dunn, 1961). The data applies to multiple samples, each with their own confidence interval, which increases the uncertainty inherent in the collective confidence intervals because of the increased risk of error from stochastic events. Bonferroni intervals (Neu *et al*., 1974; Byers *et al*., 1984) were calculated at a 95% significance to adjust the individual confidence intervals accordingly, and reduce the risk of making a Type I error (false positive, or the incorrect rejection of the null hypothesis) in drawing the ultimate conclusions.

The Wilcoxon Signed Rank (WSR) test was used to examine tick numbers between sampling periods within the respective vegetation structure units. This is the non-parametric equivalent of a paired t-test, and was deemed to be the most appropriate because the samples were assumed to be not independent (Steel and Torrie, 1980). The rationale behind this assumption is based on the occurrence of the tick numbers within the same vegetation structure units, and their exposure to the same hosts, between sampling periods. Hence, while the environmental parameters may change between sampling periods, the structural components of the tick habitat remain essentially the same.

Tick Age Classes and Vegetation Structure

Ordinarily, a two-way ANOVA would be conducted to examine the relationship between the parameters of tick age class and vegetation structure type. The data, however, is non-parametric. Hence individual KW tests for each age class between the two sampling periods and across the vegetation structure units were performed. The aim of this was to examine whether there is a statistically significant difference in tick developmental stages across the various vegetation structure types. Dunn's post-hoc test was undertaken for each significant KW test to determine where the difference lies. The Wilcoxon Signed Rank test was used to test whether there was a difference between the two sampling periods.

Diurnal Tick Activity and Vegetation Structure

Tick activity was equated to questing, with increased tick activity expressed as a higher number of ticks caught. The data were pooled, and KW tests performed to examine differences in overall tick activity between the diurnal sampling times during each sampling period. Differences in overall activity for each sampling time period between November 2014 and February 2015 were tested using WSR test.

Individual KW tests for the each period of activity between the two sampling periods and across the vegetation structure units were performed. Dunn's post-hoc test was undertaken for each significant KW test to determine where the variance responsible for any observed differences lay. The WSR test was used to test the difference between the results obtained for the two sampling periods.

Eland Space Use Pattern

The selection or avoidance of eland for various vegetation structure types for both sampling periods, and across the two preceding seasons, was examined to determine the influence of the late season fire on animal movement patterns, as well to provide a resource-use context against which to compare any observed response to tick abundance. This was tested using the chi-square (χ^2) test (Steel and Torrie, 1980). Bonferroni confidence intervals were

subsequently calculated at the 95% level (Neu *et al*., 1974; Byers *et al*., 1984) to determine the significance of structure type preference or avoidance. It should be noted that the November 2013 dataset is substantially smaller than the February 2014 dataset because the eland spent most of the time on a neighbouring property. This was not included in the vegetation mapping, and hence these data were excluded. Eland also frequented the wetland habitat, which was not sampled for ticks and hence also excluded.

The hypothesis that eland utilize areas with the lowest tick abundance during the summer months was also tested using the chi-square test and by calculating the Bonferroni confidence intervals at the 95% significance level. The tick numbers recorded per drag, allied to the GPS data for each drag transect, allowed the tick abundance for each polygon to be mapped according to five abundance classes (Table 2). Eland location data could then be overlain against this GIS layer, facilitating chi-squared analysis to test whether eland respond spatially to tick abundance.

Table 2: Classes applied to tick abundance

Tick Abundance Class	Total Number of Ticks	Number of Adult Ticks
Low	0-250	0-30
Moderately Low	251-500	31-60
Moderate	501-750	61-90
Moderately High	751-1000	91-120
High	≥1001	>121

Assuming that adult ticks are more visible to eland, and the link between adult tick abundance and intense discomfort is more readily discernible to the animal, it was concluded that eland may respond primarily to adult tick abundance as opposed to total tick abundance. The analysis was repeated, with the adult tick abundance in each polygon classified according to Table 2. Few adult ticks were collected during the November sampling period, and therefore the analysis was restricted to the February sample period.

7. RESULTS

7.1 Vegetation Structure Types at Kgaswane Mountain Reserve

The dominant structural type within the study area is the Short Upland Grassland (SUG), which occupies the quartzitic ridges in the uplands of the western and central parts of the reserve (Figure 6). The vegetation is homogenous and dominated by *Loudetia simplex, Panicum coloratum* and *Themeda triandra*. The structural unit covers an area of approximately 2074.5ha, or 44.6% of the reserve (Table 3).

The lower lying areas of the upland core of the reserve consist of the second largest structure type, namely Tall Upland Grassland (TUG) (Figure 6, Table 3). This is also remarkably homogenous in structure, and cover 857ha, or 18.4% of the study area. The structurally most heterogeneous vegetation units are located in the eastern valley section of the reserve (Figure 6). The herbaceous pattern is repeated within the tall open woodland categories that dominate this landscape, with short, sourveld grass species dominating the hill crests and higher areas and the more stemmy *Andropogonoid* species such as *Hyperthelia dissoluta* occurring lower down on the catena. The lower altitude allows a scattered tree layer to establish a more stratified vegetative structure. The open woodland type is equally distributed between the short and tall grass constituents, and each covers approximately 10% of the study area (Table 3).

The Tall Closed Woodland (TCW) is the most fragmented of the structure types (Figure 6). In the eastern valley it occupies mainly the foot-slope areas of the topography adjacent to valley bottoms. On the upland plateau the structural unit is confined to narrow, steep-sided valleys, although there are two large patches: one at the head of the wetland and one dominating the fire-exclusion zone of a valley network. Approximately 14% of the reserve is composed of this structure type (Table 3). The two smallest structure types are the Shrubland with a tall grass layer (ST) on the lower slopes of the central east-facing catena; and the Tall Lowland Grassland (TLG) that generally occupies the main valley floor (Figure 6). Each of these structural types comprises between 1 and 2 percent of the study area (Table 3).

Table 3: Area contributions of the various vegetation structure types found in the Kgaswane Mountain Reserve, in hectares and proportions of the total area.

Structure Type	Area (ha)	Percentage	Proportion
Short Upland Grassland (SUG)	2 074.50	44.64	0.45
Tall Upland Grassland (TUG)	857.70	18.46	0.18
Tall Lowland Grassland (TLG)	72.80	1.57	0.02
Shrubland; Tall Grass Layer (ST)	43.20	0.93	0.01
Tall Closed Woodland (TCW)	639.90	13.77	0.14
Tall Open Woodland; Tall Grass (TOWT)	434.00	9.34	0.09
Tall Open Woodland; Short Grass (TOWS)	468.90	10.09	0.10
Wetland	55.70	1.20	0.01
Totals	**4 646.70**	**100.00**	**1.00**

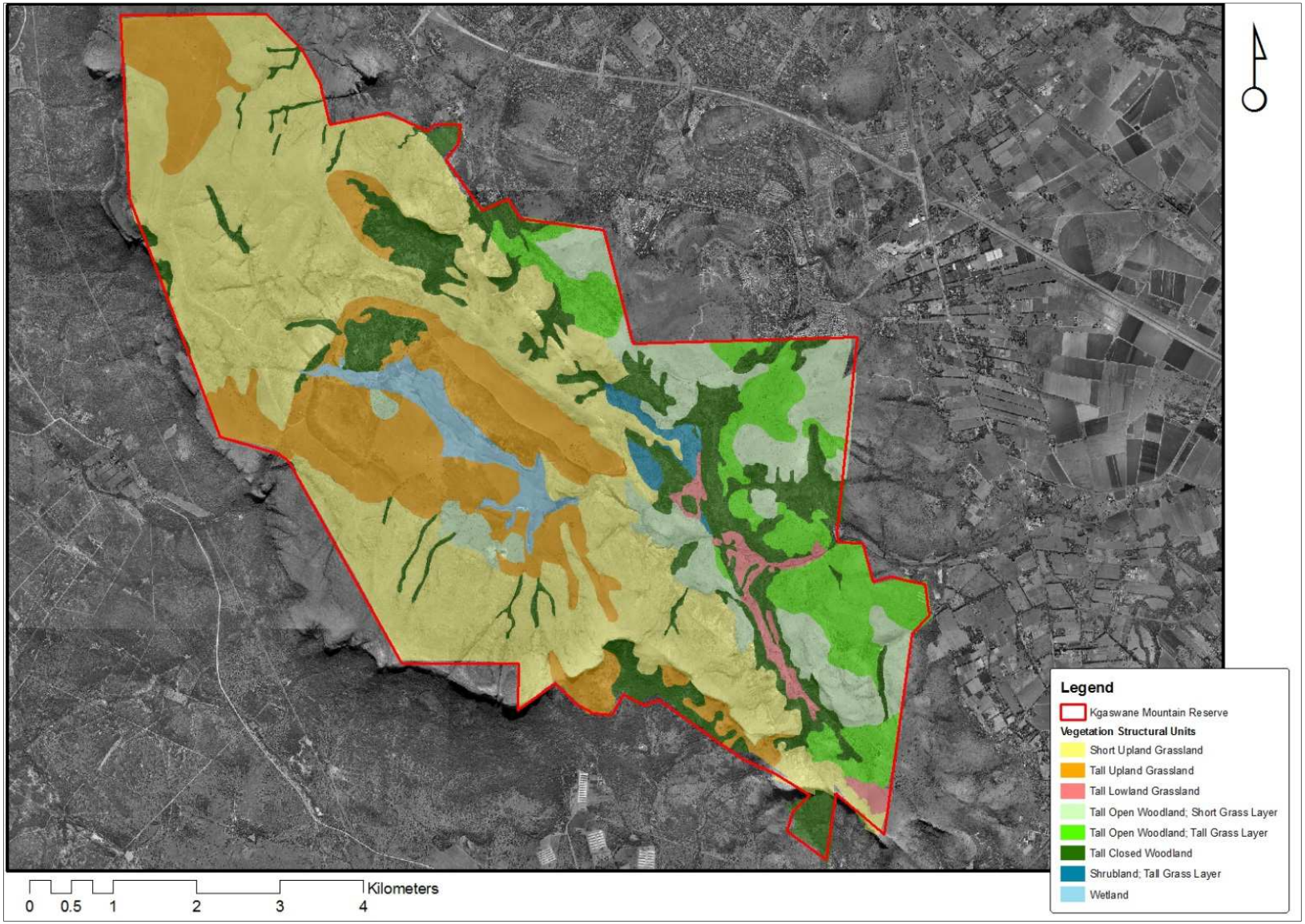


Figure 6: Vegetation structure types of Kgaswane Mountain Reserve.

7.2 Tick Abundance and Vegetation Structure

As was anticipated, the Shapiro-Wilk test revealed that all but three of the samples had data that are not normally distributed ($p<0.05$). The skewed data distribution is evident in Figure 7, with the consistent pattern being the similar number of ticks per drag in the lower three quartiles and the large variation in the number of ticks caught per drag in the fourth quartile of each sample. This is particularly exaggerated in the TUG during the second sampling period (Figure 7).

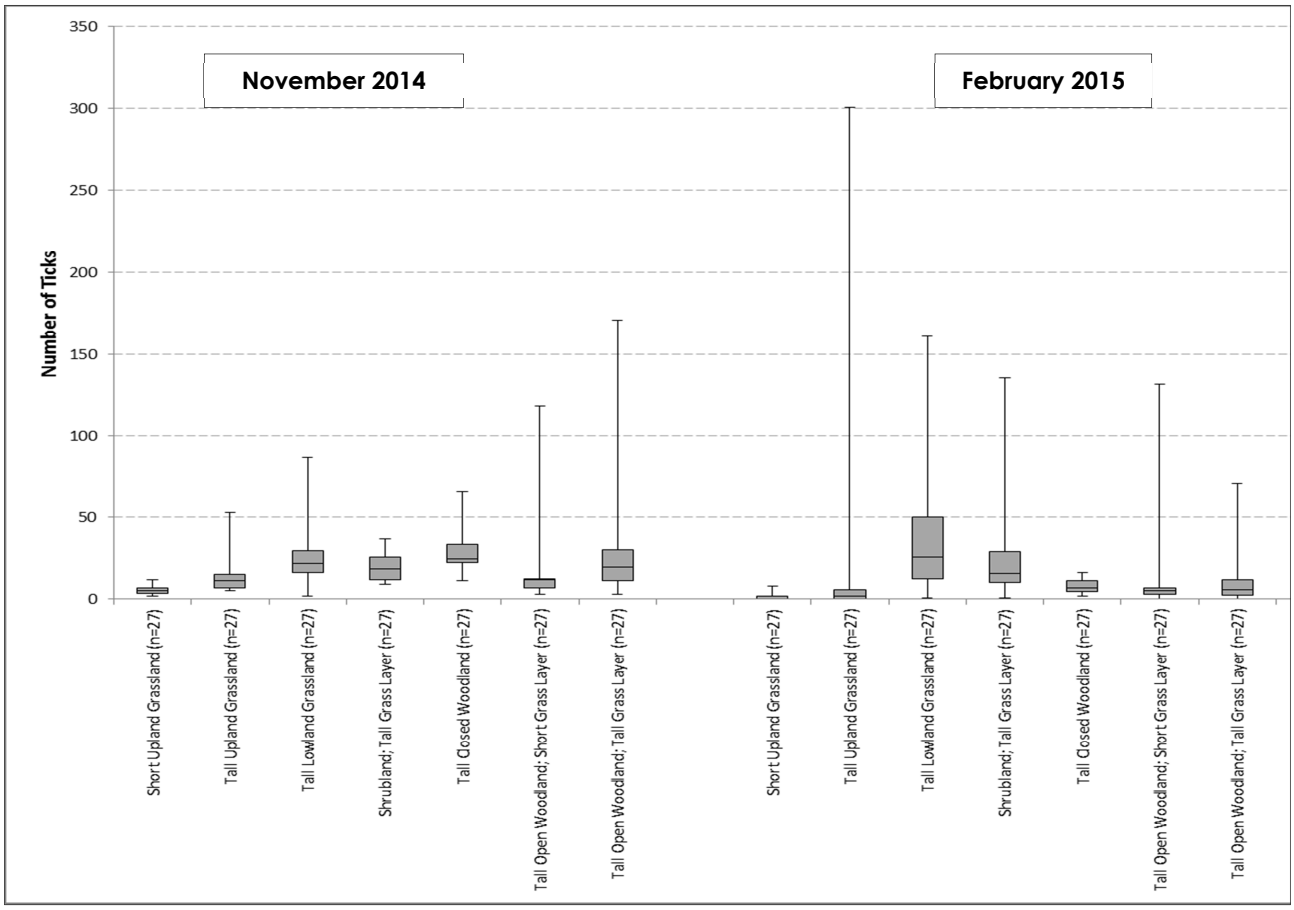


Figure 7: Boxplot showing tick capture data for the various vegetation structure types during the two sample periods.

During the first sampling period, in November 2014, 3 696 ticks were collected; while 3 168 ticks were collected in February 2015, the second sampling period. There were significant differences in tick abundance across the structural types for both seasons (KW test-November: $H=85.09$; $df=6$; $p\leq0.01$; February: $H=90.70$; $df=6$; $p\leq0.01$; Figure 8).

Not only did the numbers vary, but the distribution of ticks across the landscape tended to be more localized and aggregated during the February sampling period as the

standard error of mean tick numbers per drag is notably smaller (with the exception of the TOW(T) areas) and more consistent across the structure types (Figure 8). The TLG and TUG areas in particular display a high mean variation between the samples. This reflects the high incidence of single ticks collected during late summer, and the influence of localised individual aggregations of tick larvae on the data. During November the bulk of the ticks sampled were larvae that are still grouped following their hatching.

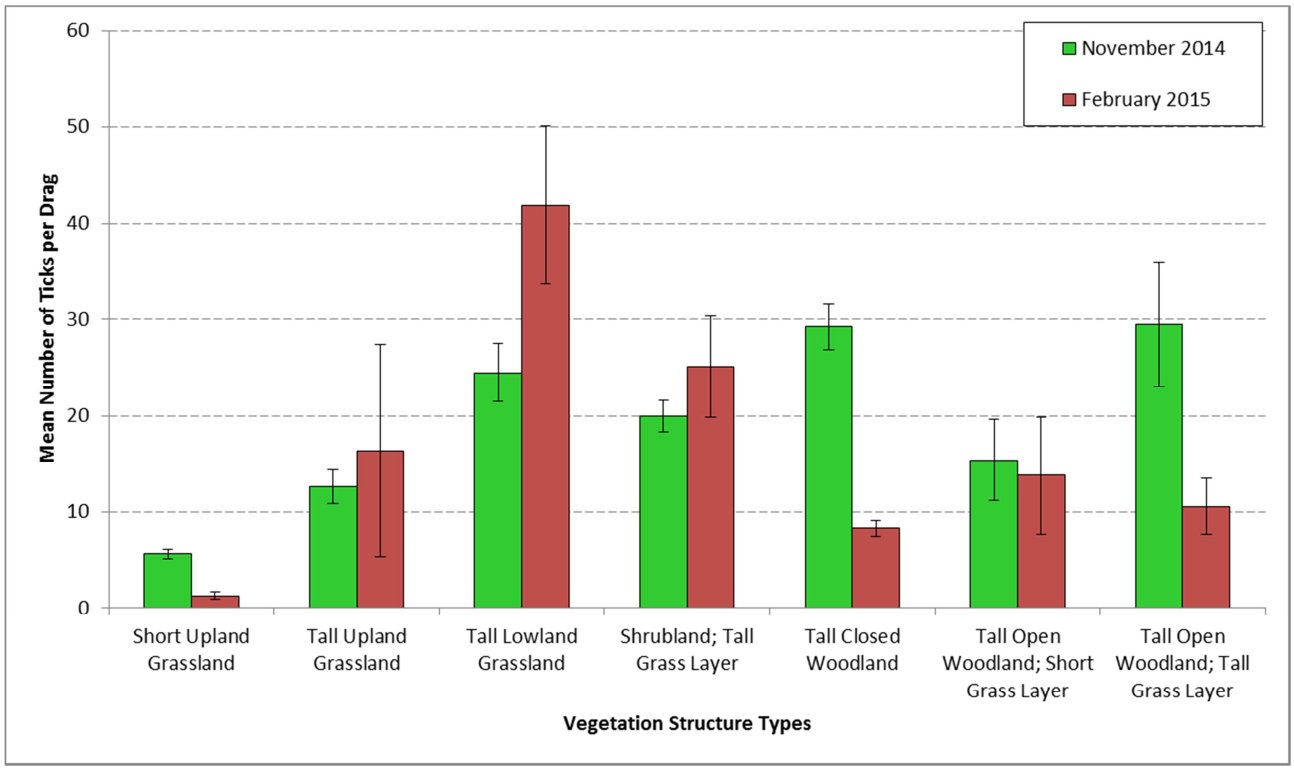


Figure 8: Mean number of ticks per drag for the respective sampling periods November 2014 and February 2015. Error bars indicate standard error.

In the early wet season (November 2014) the highest tick numbers were found in the areas with tall vegetative cover where the sheltered conditions can be expected to be more conducive to tick survival (Figure 8). The TCW and TOW(T) supported the highest total tick numbers, followed by the TLG and ST respectively (Figure 8, Table 4). The dominant pattern to emerge is that of consistently fewer ticks being caught in the SUG areas relative to the other structure types (Dunn's test; $p \leq 0.01$; Table 4; Figure 8), reflecting either high tick larvae mortality through desiccation on the exposed slopes, or a dearth of host traffic in these areas. The TUG also had significantly fewer ticks than the more sheltered structure types (Figure 8; Table 4). The TLG and TCW yielded a significantly greater number of ticks than TOW(S) during the November sampling period (Dunn's Test; $p \leq 0.05$; Table 4; Figure 8).

Table 4: Results of the multiple paired comparisons (Dunns Test) during the two sampling periods. The two-sided Bonferrini z-values are 3.038 (0.05 confidence level) and 3.494 (0.01 confidence level).

	SUG	TUG	TLG	ST	TCW	TOW(S)	TOW(T)
November 2014							
SUG	-						
TUG	2.907	-					
TLG	6.397**	3.49*	-				
ST	5.695**	2.789	0.702	-			
TCW	7.74**	4.833**	1.343	2.045	-		
TOW(T)	2.888	0.019	3.509**	2.807	4.852**	-	
TOW(S)	5.778**	2.871	0.619	0.082	1.963	2.889	-
February 2015							
SUG	-						
TUG	2.297	-					
TLG	7.993**	5.695**	-				
ST	7.189**	4.892**	0.804	-			
TCW	4.712**	2.414	3.281*	2.478	-		
TOW(T)	3.464*	1.167	4.529**	3.725**	1.248	-	
TOW(S)	4.192**	1.894	3.801**	2.998	0.520	0.728	-

* = significant at $p \leq 0.05$

** = significant at $p \leq 0.01$)

The occurrence of a significant proportion of the seasonal rainfall by February is expected to manifest itself unevenly across the vegetation types, as the dual influence of dense, stratified cover and deeper, heavier soils create more humid conditions at sward level in the TLG and ST structure types. In the February 2015 sampling period, the TLG supported the highest tick numbers by a substantial and significant margin (Dunn's test; $p \leq 0.01$; Table 4), representing an increase of nearly 100% from the previous sampling period (Figure 8). The improved conditions for tick survival are also reflected in the greater tick numbers found in the sheltered TCW and ST structure types compared to the upland grassland types (Dunn's test; $p \leq 0.01$; Table 4; Figure 8). The SUG again contained significantly lower tick numbers than the other structure types (Dunn's test; $p \leq 0.01$; Table 4; Figure 8), reflecting continued

malign conditions for tick survival in spite of the occurrence of rainfall. There was no difference in tick numbers between the upland grassland types (Table 4).

There were, in general, significant differences in tick abundance within the vegetation structure types between the two sampling periods (Table 5). The SUG yielded significantly more ticks in early summer than later on (WSR test; $p \leq 0.01$; Table 5), while the TUG and TLG areas yielded greater numbers of ticks later on in the season (WSR test; $p \leq 0.05$; Table 5; Figure 8). There was no significant difference in tick numbers in the ST between the two sampling periods (Table 5), suggesting a more constant micro-climate. An unexpected trend was evident among the tall woodland structure types, with tick numbers significantly lower after the bulk of the summer rainfall had occurred (Table 5; Figure 8).

Table 5: Results of the Wilcoxon's Signed Rank Test, showing the differences in tick abundance for the respective vegetation structure units between the early and later rainfall periods (n=27; α(0.05) = 107; α(0.01) = 83). (Note: Unlike the KW and Dunn's tests, if the test statistic is greater than the critical value, the underlying hypothesis of an existing relationship is rejected, and the result is not significant).

Vegetation Type	Test Statistic	Significance
SUG	12	$p \leq 0.01$
TUG	93	$p \leq 0.05$
TLG	106	$p \leq 0.05$
ST	173	N.S.
TCW	1	$p \leq 0.01$
TOW(T)	90	$p \leq 0.05$
TOW(S)	32	$p \leq 0.01$

7.3 Tick Age Classes and Vegetation Structure

The dominant observations made during the course of the fieldwork were:

a) The virtual absence of adult ticks during the November sampling period;
b) The dominance of tick larvae across both sampling periods; and
c) The virtual absence of nymphs during the late summer period in February (Figures 9 and 10).

The February period was characterized by a small number of drags that yielded large larval counts, as opposed to the November period where the larvae were distributed more

consistently across the drags (Figure 9). During the November sample 2 557 of the ticks caught were larvae, representing approximately 69% of the total caught. The remainder of the ticks caught consisted of 1 126 nymphs, approximately 30% of the total, and 13 adults, or approximately 0.4% of total captures. The following February the proportion of tick larvae trapped had increased to 87%, although the overall number was similar at 2 777. Considerably more adults, 365 individuals, were caught during this time period (Figure 9). Only 26 nymphs were recorded, constituting approximately 0.8% of the ticks caught during this period (Figure 9).

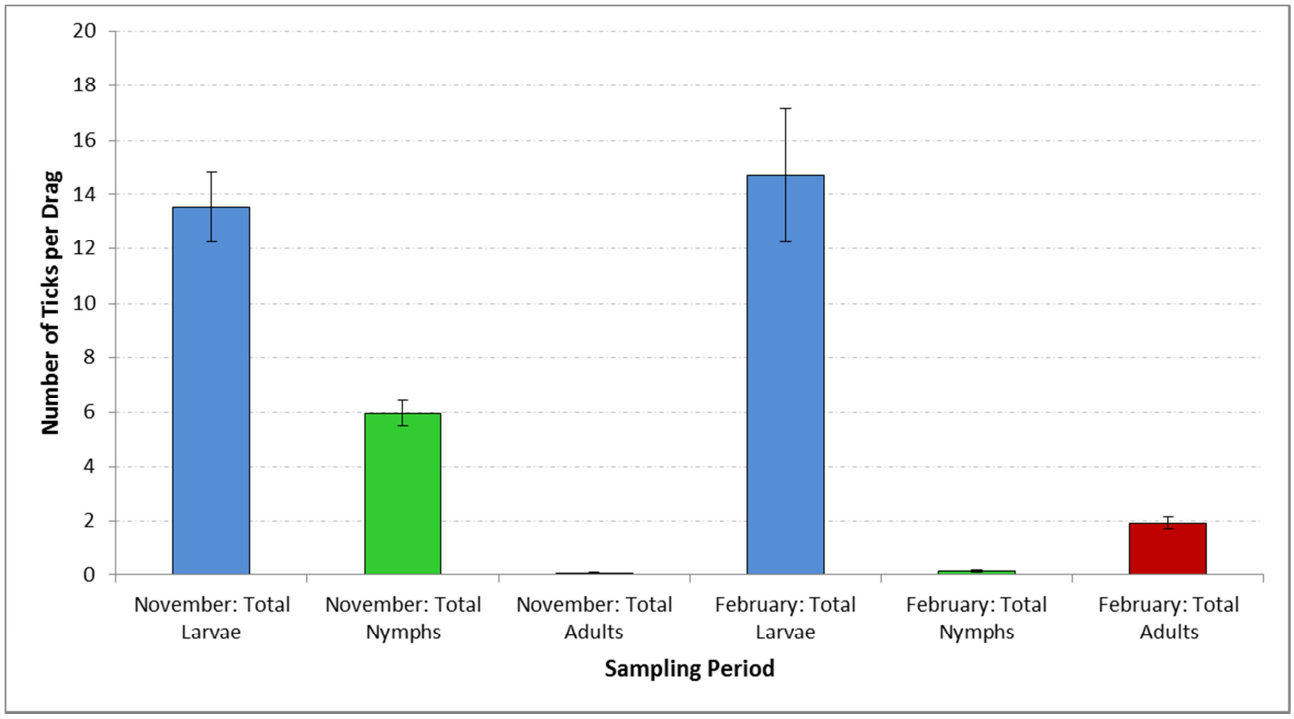


Figure 9: Mean number of ticks per drag of each developmental stage between the respective sampling periods. Error bars indicate standard error.

The occurrence and number of tick larvae and tick nymphs was strongly influenced by vegetation structure during the November sampling period (KW test: H (larvae) =80.3; df=6; $p \leq 0.01$; H (nymphs) = 53.5; df=6; $p \leq 0.01$; Figure 10). Adult ticks were present during this period, but there was no statistical evidence suggesting that their occurrence favoured particular vegetation structure types. Tick larvae and adult numbers during the February sampling period were significantly linked to vegetation structure (KW test: H (larvae) =64.08; df=6; $p \leq 0.01$; H (adults) = 110; df=6; $p \leq 0.01$; Figure 10) although there was no clearly evident influence of vegetation structure on nymph numbers.

When compared against most of the other vegetation types, there is a significant negative relationship between tick larvae and the SUG in both of the sampling periods

(Dunn's test; $p \leq 0.01$; Appendix: Table I), although there is no difference in tick larvae numbers between the SUG and TUG. There is a strong affinity between tick larvae and the TLG during the later rainy season (Dunn's test; $p \leq 0.01$; Appendix: Table I), and the significant relationship identified by the KW test is mostly composed of the difference in tick numbers between TUG and all the other structure types. The TCW and TOW(T) had the highest number and proportion (25%) of tick larvae caught during November (Dunn's test; $p \leq 0.01$; Appendix: Table I; Figure 10). This is to be expected as they also yielded the highest overall tick numbers.

Although tick larvae were still the most numerous age class during the February sampling, the bulk of these were concentrated in the TLG and ST structure types (Dunn's test; $p \leq 0.01$; Appendix: Table I; Figure 10). The tick populations in both tall grassland structure types were overwhelmingly dominated by larvae (approximately 98% in both cases). The highest numbers of nymphs were recorded in the more sheltered structure types, such as TLG (approximately 47% of ticks caught) and ST (42%) (Dunn's test; $p \leq 0.01$; Appendix: Table II). Tick nymphs were significantly less numerous in the SUG during the November sampling period than they were in the other structure types (Dunn's test; $p \leq 0.01$; Appendix: Table II).

There were significantly more adult ticks in the ST and TCW areas during February 2015 than there were in the other vegetation structure types (Dunn's test; $p \leq 0.01$; Appendix: Table III). There was no significant difference in the number of adults caught between these two structure types (Appendix: Table III). The adult ticks were mostly concentrated in the ST and TCW structure types where they constituted 26% and 52% of the tick populations respectively (Figure 10). These two structure types yielded 80%, or 295 of the 365, adult ticks caught during the February sampling period.

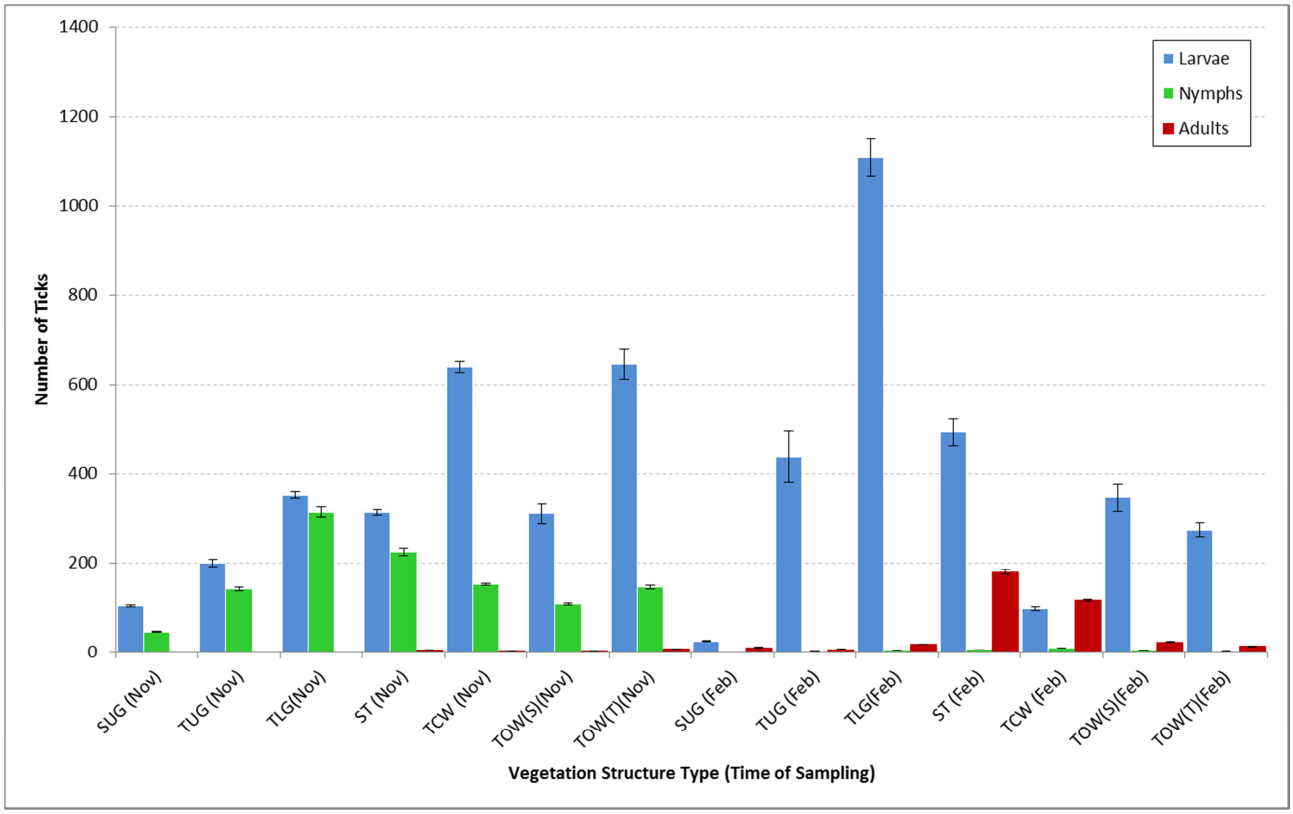


Figure 10: The different stages of development constituting the total tick counts in November 2014 and February 2015. Error bars indicate standard deviation.

The pattern of tick abundance across the life stages shifted slightly during the later stages of the rainfall season, with higher numbers of tick larvae found in the vegetation structure types characterized by tall, dense herbaceous cover. The variation within sampling units also increased substantially, showing greater disparity between tick counts (Figure 10) and suggesting an increasingly clumped distribution of tick larvae across the landscape. The standard deviations for the nymph and adult tick data were consistently smaller than that of the larvae data, indicating that these age groups are more evenly distributed, or effectively dispersed (Figure 10).

There was a significant difference in the number of larvae caught between the two sampling periods in the SUG, TLG, TCW and TOW (T) structure types (WSR Test; $p \leq 0.01$; Table 6). In the case of the SUG and TCW, the number of larvae caught in the early rainfall period was significantly lower than that of the later rainfall period, and *vice versa* for the TLG and TOW(T) (Figure 10; Table 6).

Table 6: Results of the Wilcoxon's Signed Rank Test, showing the statistical significance of the differences in the numbers of ticks caught within the three developmental stages between the two sampling periods (n=27; α(0.05) = 107; α(0.01) = 83). (Note: Unlike the KW and Dunn's tests, if the test statistic is greater than the critical value, the underlying hypothesis of the parameters being related is rejected, and the result is not significant).

	Larvae		Nymphs		Adults	
Vegetation Type	**Test Statistic**	**Significant**	**Test Statistic**	**Significant**	**Test Statistic**	**Significant**
SUG	7	p≤0.01	6	p≤0.01	0	p≤0.01
TUG	130	N.S.	1	p≤0.01	0	p≤0.01
TLG	40	p≤0.01	1	p≤0.01	0	p≤0.01
ST	161	N.S.	0	p≤0.01	0	p≤0.01
TCW	1	p≤0.01	0	p≤0.01	0	p≤0.01
TOW(T)	145	N.S.	1	p≤0.01	12	p≤0.01
TOW(S)	41	p≤0.01	1	p≤0.01	98	p≤0.05

The conspicuously low number of nymphs encountered during the February 2015 sampling period accounts for the significant differences ($p \leq 0.01$) in nymph numbers within the various structure types between the two sampling periods (Table 6). Adult tick numbers were significantly lower prior to the onset of the rainfall period ($p \leq 0.01$; Table 6), reflecting the seasonal nature of tick recruitment.

7.4 Diurnal Tick Activity and Vegetation Structure

Overall Tick Activity

The data did not support the hypothesis that there were significant differences in overall tick activity between the diurnal times during November 2014 and February 2015 (KW-November; H=5.978, df = 2, all comparisons p >0.05; KW-February; H=5.991, df = 2, all comparisons p >0.05). The patterns of collective diurnal tick activity appeared constant across both sampling periods (WSR Test, α (0.05) = 146.06; all comparisons p>0.05). The trends identified were not significant, possibly because many of the differences observed could be attributed to increased variability in the upper quartile, which did not affect the rankings used in the statistical tests (Figure 11).

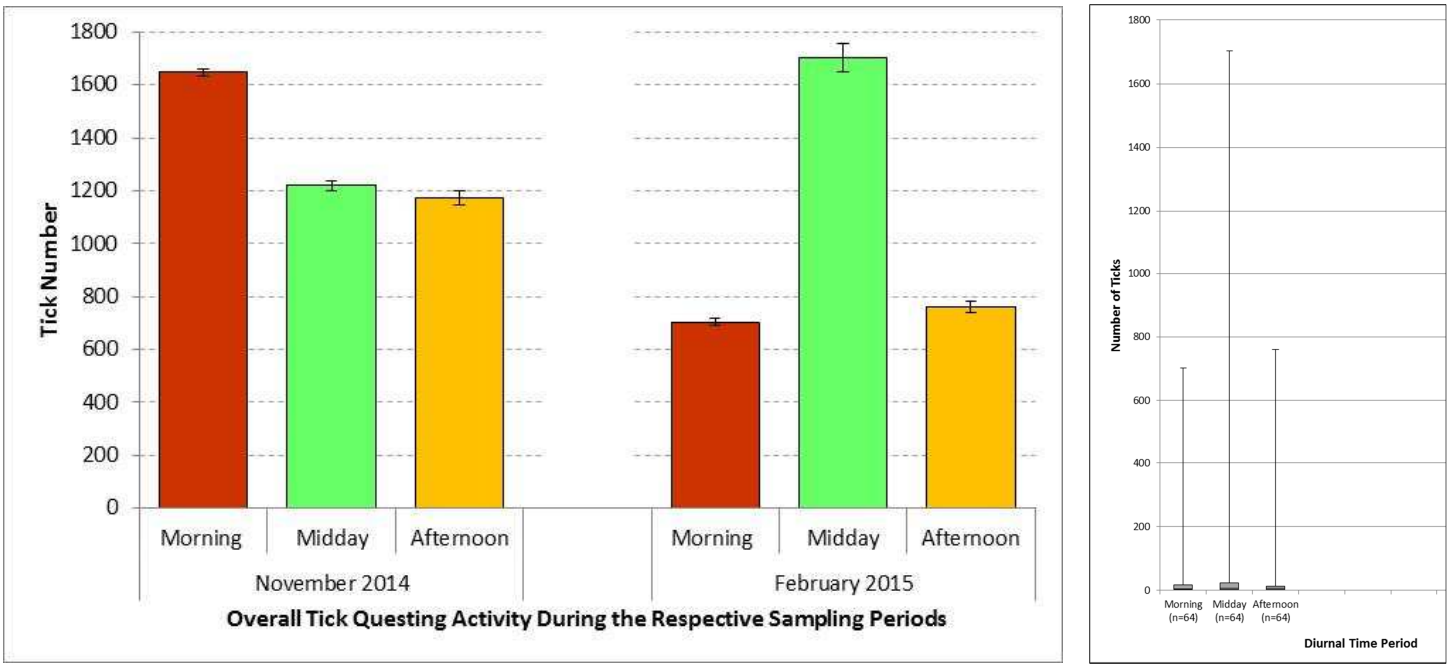


Figure 11: Overall tick activity across all vegetation structure types, shown in total tick counts (left). Error bars indicate standard deviation. The boxplot (right) indicates the spread of the upper quartile of the February 2015 data.

Tick Activity Between Diurnal Time Periods Within Vegetation Structure Types

Several vegetation structure types indicated differences in tick activity between the diurnal time periods (KW test, df = 2; $p \leq 0.01$; Table 7). There was, however, little evidence of a pattern linking tick activity across similar structural components (Figure 12). For example, tick activity in the TUG during November was significantly less during midday than either the morning or afternoon sessions (which yielded the same activity) (Dunn's test; $p \leq 0.01$). However, the same pattern was not evident in the other grassland structure types, SUG and TLG. Likewise, the ST in November yielded lower activity levels in the afternoon than during the morning or midday periods, which showed the same activity levels (Dunn's test; $p \leq 0.01$), but the pattern was not repeated in the TCW, as one would have expected had there been a consistent influence exerted by structure. It is fair to say, however, that tick activity was more consistently evenly distributed across the morning, midday and afternoon periods for each structure type in February than in November (Table 7).

Table 7: Results of the Kruskal-Wallis tests examining the differences in tick activity between the morning, midday and afternoon times within each vegetation structure type during November 2014 and February 2015 (n=3, df=2; Critical H (0.01) = 9.21; Critical H (0.05) = 5.99).

	Sample Period			
	November 2014		February 2015	
Vegetation Structure Type	Test Statistic (H)	Significance	Test Statistic (H)	Significance
SUG	0.59	NS	0.35	NS
TUG	16.30	$p \leq 0.01$	3.43	NS
TLG	2.81	NS	5.71	NS
ST	12.84	$p \leq 0.01$	0.26	NS
TCW	1.88	NS	0.20	NS
TOW(S)	16.13	$p \leq 0.01$	6.28	$p \leq 0.05$
TOW(T)	2.54	NS	5.12	NS

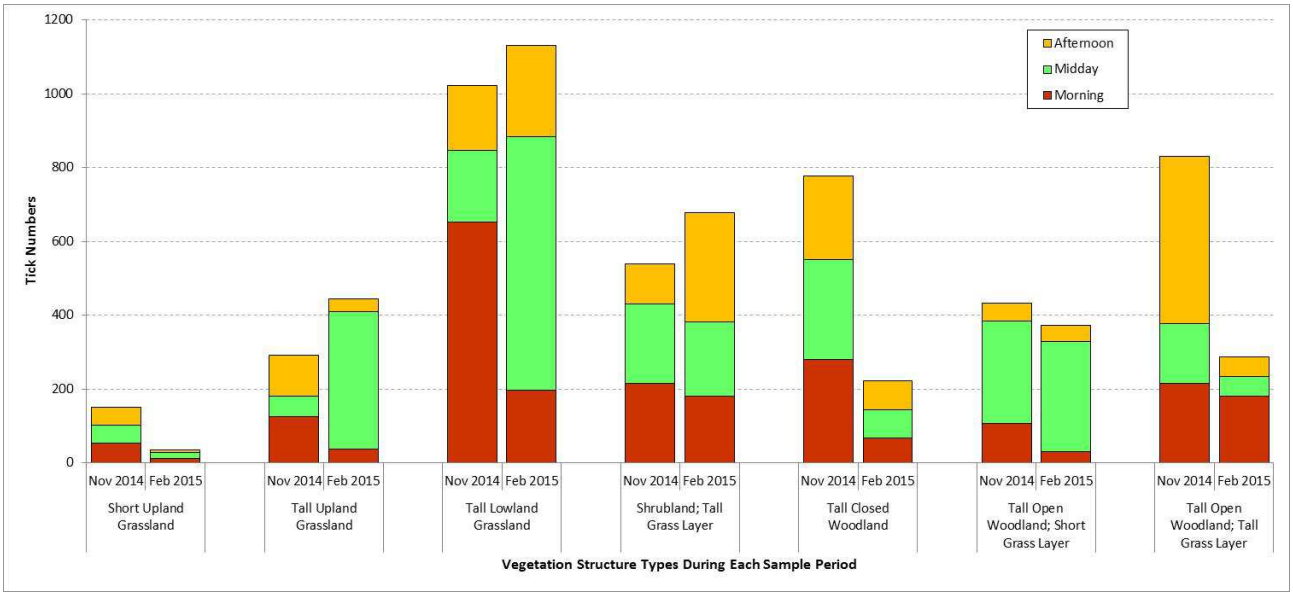


Figure 12: Diurnal tick activity for all seven structure types across the two respective sample periods.

Tick Activity Between Vegetation Structure Types

There were significant differences in tick activity between the vegetation structure types for each of the diurnal time periods for the November 2014 and February 2015 sampling periods (KW test; $p \leq 0.01$; Table 8). Most of this variance was attributed to the substantially fewer ticks caught in the SUG, and to a lesser extent the TUG, for each of the diurnal time periods sampled.

Table 8: Results of the Kruskal-Wallis tests examining the differences in tick activity during the morning, midday and afternoon time periods between the vegetation structure types during November 2014 and February 2015 (n=7, df=6; Critical H (0.01) = 16.812).

	Sample Period			
	November 2014		February 2015	
Diurnal Time Period	**Test Statistic (H)**	**Significance**	**Test Statistic (H)**	**Significance**
Morning	42.66	$p \leq 0.01$	38.69	$p \leq 0.01$
Midday	37.25	$p \leq 0.01$	25.29	$p \leq 0.01$
Afternoon	37.304	$p \leq 0.01$	36.403	$p \leq 0.01$

Significantly fewer ticks were trapped in the morning in the SUG than in the more dense lowland structure types (Dunn's test; $p \leq 0.01$; Appendix Table IV). In February this pattern extended to the TUG. There was no difference in morning tick activity between the two upland grassland types for both sampling periods.

In November the upland grassland types yielded lower tick numbers during the midday time period than the TLG and denser woodland types (Dunn's test; $p \leq 0.01$; Appendix Table V). Midday tick activity was more consistent across structure types in February. The only significant differences identified were between the SUG, with the least ticks captured, and the two dense lowland woodland types (Dunn's test; $p \leq 0.01$; Appendix Table V; Figure 12).

With the exception of the SUG, and TUG in February, there was no difference in afternoon tick activity among the vegetation structure types. The SUG had significantly lower levels of afternoon activity than several of the denser structure types (Dunn's test; $p \leq 0.01$; Appendix Table VI; Figure 12).

Tick Activity Between Vegetation Structure Types Across the Two Sample Periods

Morning and afternoon tick activity was significantly lower in the upland grassland structure types in February than in November (WSR test; $p \leq 0.01$, Table 9, Figure 12), which is the opposite to what would have been expected. The denser lowland structure types showed little or no difference in tick activity patterns between November and February (Table 9), indicating sheltered, more stable environmental conditions. There were higher levels of tick activity recorded in November than in February for all time periods in the TCW ($p \leq 0.01$; Table 9).

Table 9: Results of the Wilcoxon Signed Rank Tests exploring the differences in tick activity within vegetation structure types and between sampling periods. (n=9; Critical Value α(0.05) = 6; Critical Value α(0.01) = 2). (Note: Unlike the KW and Dunn's tests, if the test statistic is greater than the critical value, the underlying hypothesis of the parameters being related is rejected, and the result is not significant).

Vegetation Structure Type	Morning Test Statistic	Midday Test Statistic	Afternoon Test Statistic
SUG	0**	6*	0**
TUG	1**	20#	1**
TLG	14#	2*	15#
ST	15#	18#	17#
TCW	0**	0**	1**
TOW(T)	0**	18#	17#
TOW(S)	15#	3*	1**

* = significant (p = 0.05)

** = significant (p = 0.01)

= Not Significant

7.5 Eland Movement and Tick Abundance

Eland Preference for Vegetation Structure Types

Eland were frequently encountered during the November sampling period gathered on the burned areas, and then never in a group larger than 30 animals. In contrast, during the February sampling period, the eland were observed congregated into one large herd of approximately 130 animals that remained in the upland areas in the central and western parts of the reserve. This is reflected in the GPS data (Figure 13). Several movement patterns are evident from the spatial data. The obvious one is the shift in altitude. During late summer the eland are confined exclusively to the upland areas, whereas during early summer, prior to the commencement of the rains, the eland are located in the central valley bottom for approximately 60% of the time. The eland, in fact, appear to congregate preferentially in the TLG and TCW of the valley floor.

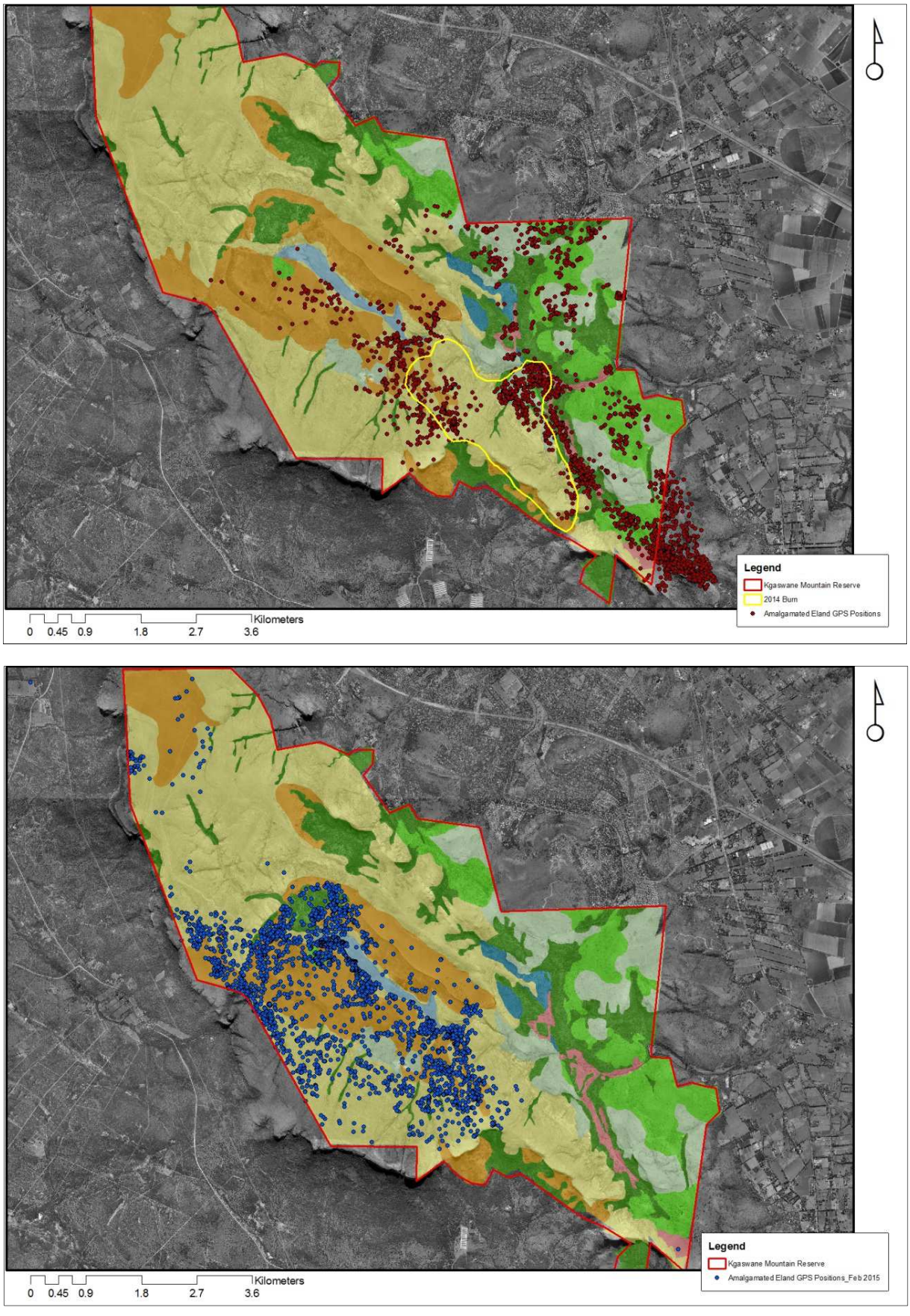


Figure 13: Shift in eland movement between the November 2014 sampling period (top), and February 2015 sampling period (bottom).

There also appears to be a change in the social behavior of the animals. The broader spread of GPS points in November suggests a greater degree of autonomy between the four collared animals and their herds. There appear to be four conglomerations of GPS points (Figure 13) in the north, central and southern portions of the reserve. The GPS points during the February sampling periods are more concentrated, suggesting that the collared animals were spending more time in close proximity to one another, corroborating the observed behaviour.

An additional pattern is evident with regards to the vegetation structure types favoured by the eland. The animals appeared to be more evenly distributed across the structure types during the November sampling period, with the exception of the ST which was avoided (Figure 14). During the February sampling period, however, they were confined virtually entirely to the upland grassland structure types (Figure 14). The TCW areas that were frequented were situated in the upland areas and surrounded by upland grasslands (Figure 14).

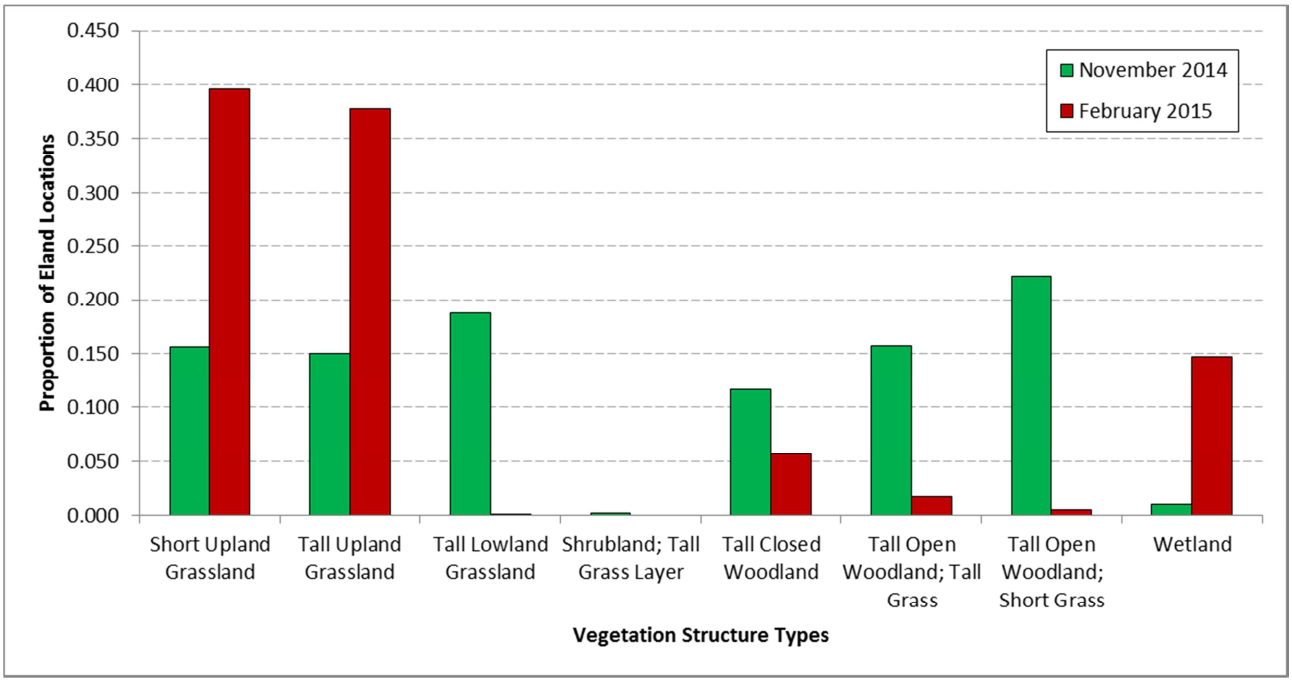


Figure 14: Proportion of eland GPS locations in each vegetation structure type during the November 2014 and February 2015 sampling periods.

There was a significant relationship between eland movement and vegetation structure type during both sample periods (χ^2 test; $p<0.001$; Table 10). In November 2014 the proportion of eland locations expected to occur in all vegetation structure types was significantly different to the observed proportions that actually occurred ($p<0.05$; Appendix:

Table VII). Eland showed a marked preference for the TLG and the tall open woodland types, and avoided the upland grassland structure types and dense ST and TCW types (Appendix: Table VII). The avoidance of the SUG and the preference of the TLG appear to contribute the most to the significant relationship identified in the χ^2 test (Table 10).

There was no significant relationship between eland and SUG during the February 2015 sample period (Appendix: Table VIII). The eland preferred the TUG during this time, and avoided the remaining structure types ($p<0.05$; Appendix: Table VIII).

Table 10: Chi-squared (χ^2) test for the selection of vegetation structure types by eland at Kgaswane Nature Reserve, using amalgamated location data for all four collared eland.

			November 2014			February 2015		
Structure Type	**Area (ha)**	**Proportion**	**Exp**	**Obs**	**Chi**	**Exp**	**Obs**	**Chi**
SUG	2074.50	0.45	978.73	342	414.2	1319.44	1354	0.9
TUG	857.70	0.19	404.66	327	14.9	545.52	1292	1021.5
TLG	72.80	0.02	34.35	411	4130.5	46.30	1	44.3
ST	43.20	0.01	20.38	4	13.2	27.48	0	27.5
TCW	639.90	0.14	301.90	254	7.6	406.99	194	111.5
TOW(T)	434.00	0.09	204.76	343	93.3	276.04	60	169.1
TOW(S)	468.90	0.10	221.22	485	314.5	298.23	19	261.4
Total	4591.00	1.00	2166.00	2166	4988.2	2920.00	2920	1636.2
Degrees of Freedom					6			6
Significance					$p<0.001$			$p<0.001$

Comparison with the Burned Area

To examine the potential confounding effect on animal movement brought about by the burn, the eland movement data for the season prior to the burn were reviewed. There are fewer sample points in this dataset because only one eland cow was collared, but similar patterns are evident. The eland generally congregated in the bottom of the large, central valley during November before moving into the uplands during February (Figure 15). There was a similar affinity for the upland grassland structure types during late summer, and tall open woodland types during the November period (Figure 16). The ST was avoided during the corresponding sample periods for both years, and the TCW was utilized slightly more in November than in February during both years (Figure 16). In common with the subsequent season, the chi-squared test revealed a strong relationship between eland location and

vegetation structure type during both sampling periods (χ^2 test; $p<0.001$; Table 11). During November 2013, as with November 2014, the eland avoided the SUG and preferred the TLG ($p<0.05$; Appendix: Table IX). Similarly, during February 2014, as with February 2015, the eland preferred the TUG, were ambivalent towards the SUG and avoided the other structure types ($p<0.05$; Appendix: Table X). These relationships contributed the most to the observed chi-squared significance. The patterns of eland resource use are considered suitably similar for both years, and there is little evidence to suggest that the fire had a significant influence on eland distribution.

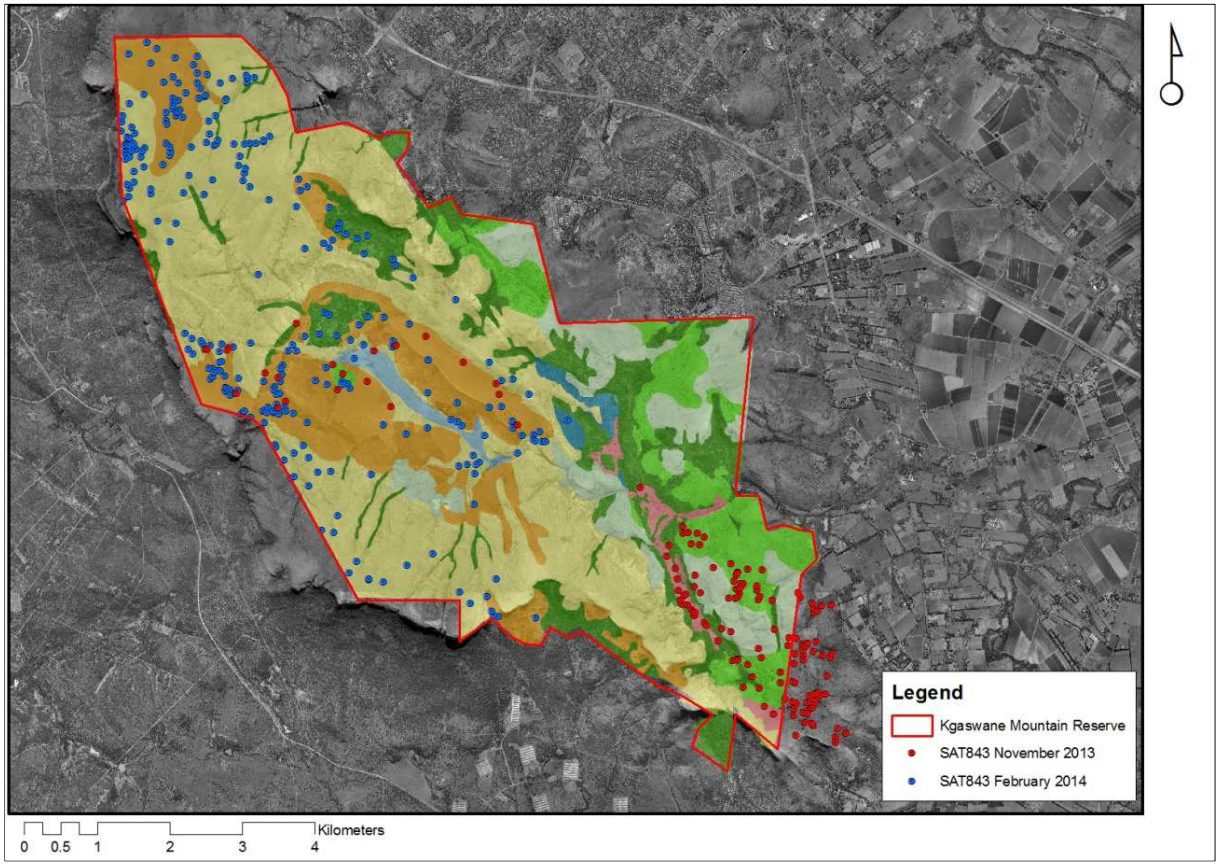


Figure 15: Shift in eland movement between the November 2013 sampling period (red), and February 2014 sampling period (blue).

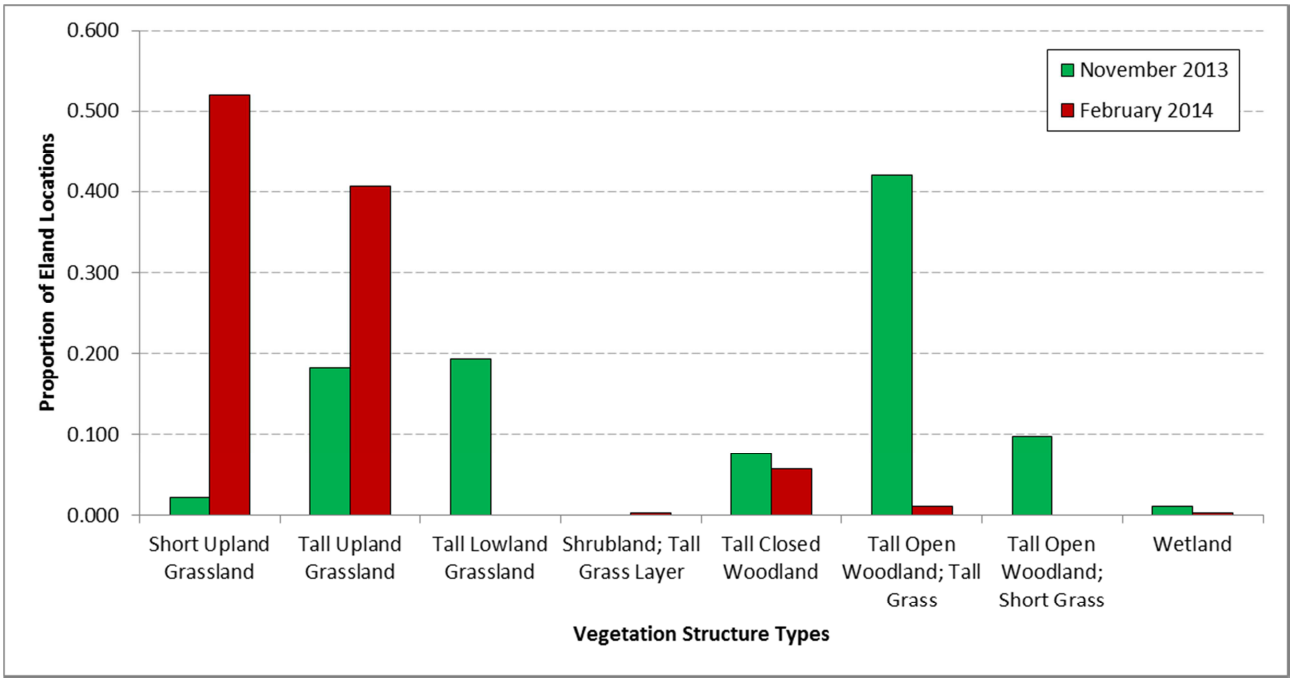


Figure 16: Number of eland GPS locations in each vegetation structure type during the November 2013 and February 2014 sampling periods.

Table 11: Chi-squared (χ^2) test for the selection of vegetation structure types by eland at Kgaswane Nature Reserve, using location data for the single collared eland.

			November 2013			February 2014		
Structure Type	**Area (ha)**	**Proportion**	**Exp**	**Obs**	**Chi**	**Exp**	**Obs**	**Chi**
SUG	2074.50	0.45	41.57	2	37.7	127.43	147	3.0
TUG	857.70	0.19	17.19	17	0.0	52.68	115	73.7
TLG	72.80	0.02	1.46	18	187.6	4.47	0	4.5
ST	43.20	0.01	0.87	0	0.9	2.65	1	1.0
TCW	639.90	0.14	12.82	7	2.6	39.31	16	13.8
TOW(T)	434.00	0.09	8.70	39	105.6	26.66	3	21.0
TOW(S)	468.90	0.10	9.40	9	0.0	28.80	0	28.8
Total	4591.00	1.00	92.00	92	334.3	282.00	282	145.8
Degrees of Freedom					6			6
Significance					p<0.001			p<0.001

The Relationship Between Eland Location and Tick Abundance

The relationship between eland November distribution and total tick abundance was significant, although the spatial patterns were not easily discernible (χ^2 test, $p<0.001$; df=5; Table 12, Figure 17). Eland favoured areas that happened to have high tick abundance, and avoided areas of moderate tick abundance ($p<0.05$; Appendix: Table XI, Figure 19). This is opposite to the expected response.

The eland appeared to be fairly evenly distributed between the upland areas of low tick abundance and high tick abundance during the February sampling period (Figure 17). Whilst there was still evidence of an influence guiding animal locations associated with tick abundance (χ^2 test, $p<0.001$; df=5; Table 12), the variation seen between the actual and expected eland observations was more evenly spread across the six tick abundance classes. The eland seemed to avoid the areas with moderately high, moderate and moderately low tick abundance ($p<0.05$; Appendix: Table XII), although this may be because they did not occur in the uplands. Eland occurred significantly more often than expected in the areas of high total tick abundance, and less often than expected in the areas of low total tick abundance ($p<0.05$; Appendix: Table XII; Figure 19). The selection by eland of areas of high total tick abundance, and avoidance of areas with low total tick numbers, is the opposite of the anticipated outcome. This suggests that the challenge provided by total tick abundance, predominantly composed of tick larvae and nymphs, is insufficient to influence animal distribution during the sampling periods.

Discarding the larvae and nymph data, and considering only adult tick abundance, revealed a stark contrast. During late summer, after the occurrence of most of the seasonal rainfall, the eland spent the majority of their time in areas with low adult tick abundance, namely the upland grassland structure types (χ^2 test, $p<0.01$; df=5; Table 12; Figure 18). The spatial pattern was obvious (Figure 18). Eland positively selected for areas with low adult tick abundance, and avoided areas with high adult tick abundance ($p<0.05$; Appendix: Table XIII; Figure 19). There was also a strong selection for the wetland habitat ($p<0.05$; Appendix: Table XIII, Figure 19), which had an unknown adult tick abundance.

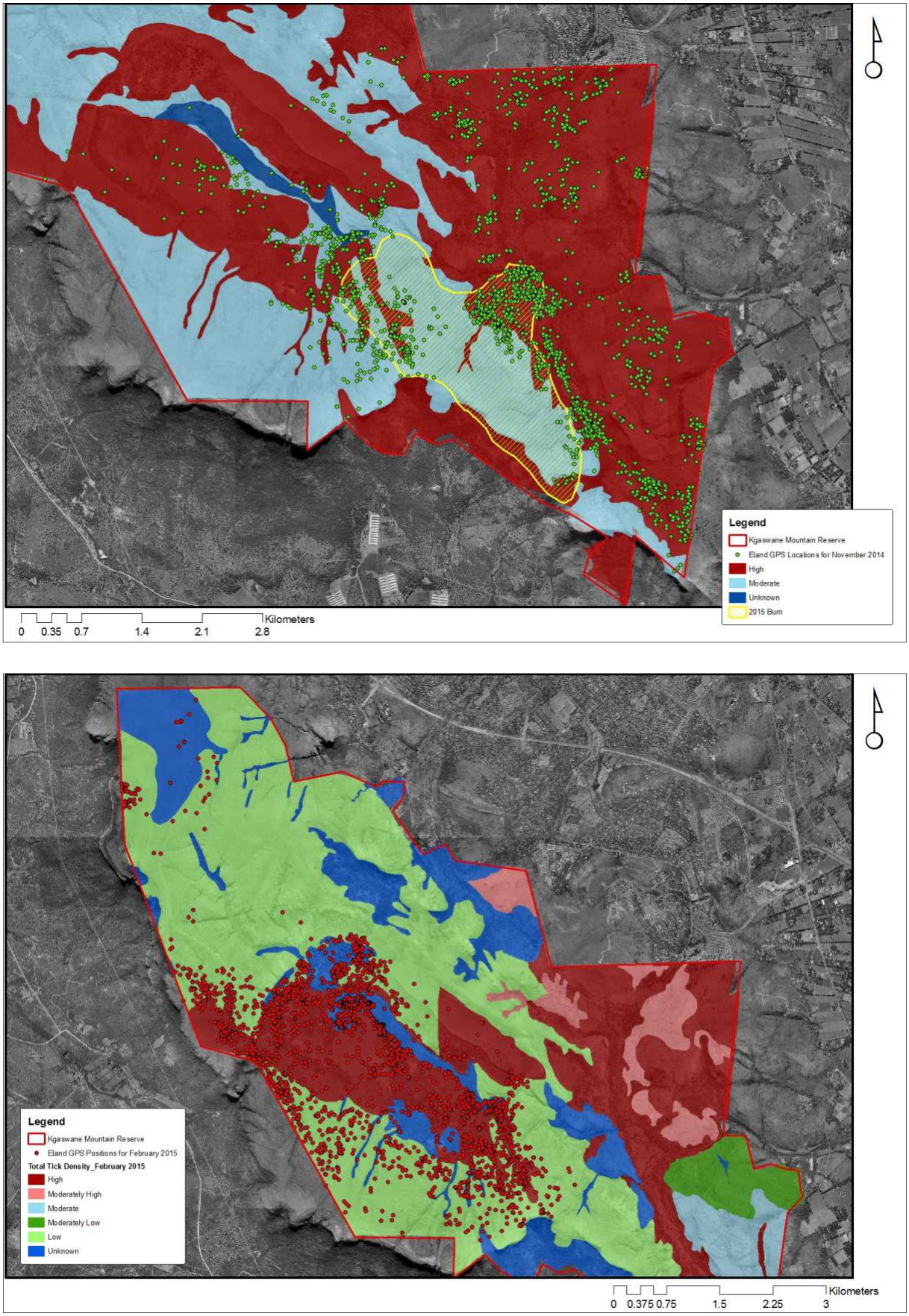


Figure 17: Eland location relative to total tick abundance for November 2014 (top); and February 2015 (bottom).

Table 12: Chi-squared (χ^2) test for the selection by eland areas of total and adult tick densities between the two sample periods. Few adult ticks were collected in November 2014, and adult tick abundance was low throughout the reserve.

Total tick abundance	Area (ha)	Proportion	Number of eland locations	Expected number of eland locations	Chi
November 2014 (Total)					
High	2516.70	0.5416	1627	1089.65	264.98
Moderately High	0.00	0.0000	0	0.00	0.00
Moderate	2074.58	0.4464	364	898.23	317.74
Moderately Low	0.00	0.0000	0	0.00	0.00
Low	0.00	0.0000	0	0.00	0.00
Unknown	55.70	0.0120	21	24.12	0.40
Total	4646.98	1.0000	2012	2012.00	583.12
Degrees of Freedom					5
Significance					p<0.001
February 2015 (Total)					
High	1146.29	0.2467	1497	843.86	505.5252
Moderately High	209.40	0.0451	0	154.15	154.1532
Moderate	140.05	0.0301	0	103.10	103.1000
Moderately Low	181.80	0.0391	0	133.83	133.8350
Low	2161.95	0.4652	1143	1591.55	126.4178
Unknown	807.56	0.1738	781	594.50	58.5081
Total	4647.05	1.0000	3421	3421.00	1081.5391
Degrees of Freedom					5
Significance					p<0.001
February 2015 (Adult)					
High	681.84	0.1467	192	501.96	191.3967
Moderately High	1.36	0.0003	0	1.00	1.0012
Moderate	0.00	0.0000	0	0.00	0.0000
Moderately Low	994.20	0.2139	18	731.91	696.3515
Low	2913.87	0.6270	2710	2145.13	148.7461
Unknown	55.70	0.0120	501	41.01	5160.2119
Total	4646.97	1.0000	3421	3421.00	6197.7074

Degrees of Freedom	5
Significance	p<0.001

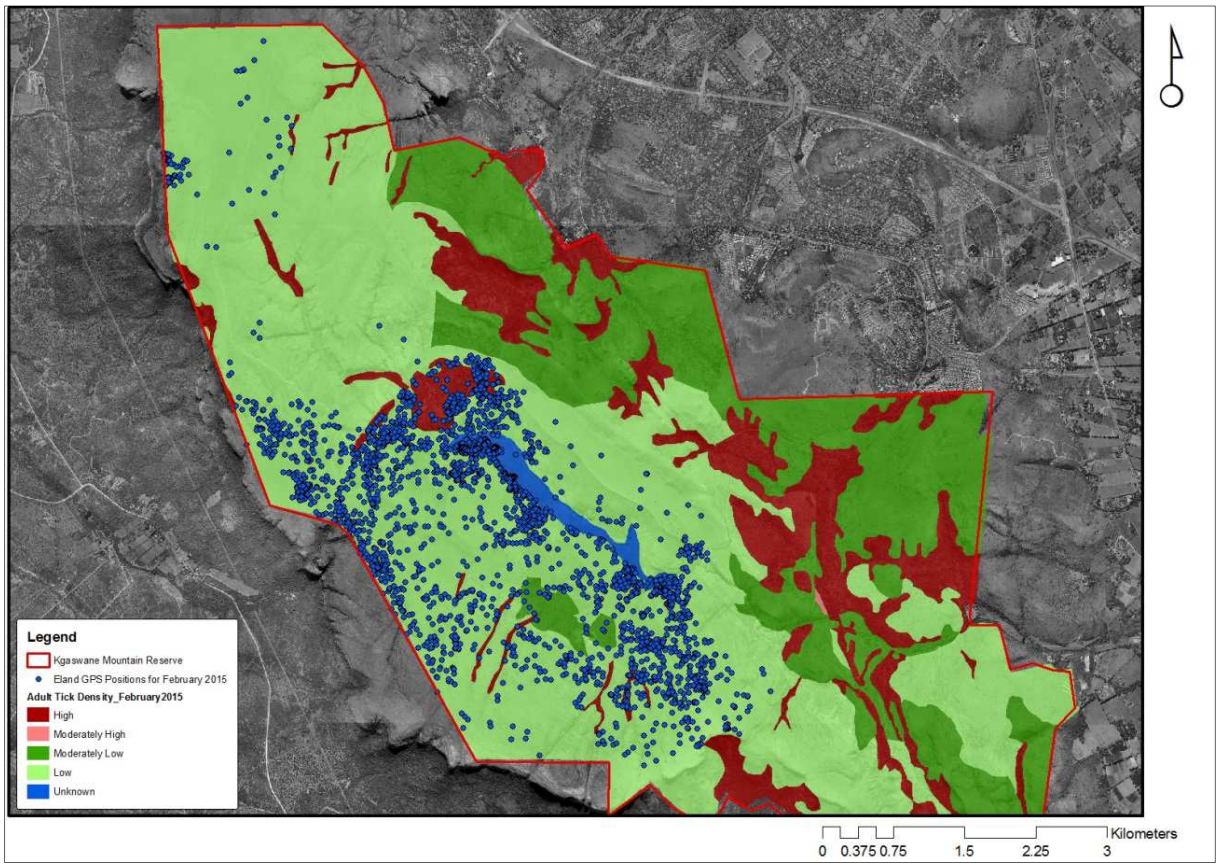


Figure 18: Eland location relative to adult tick abundance during the February 2015 sample period.

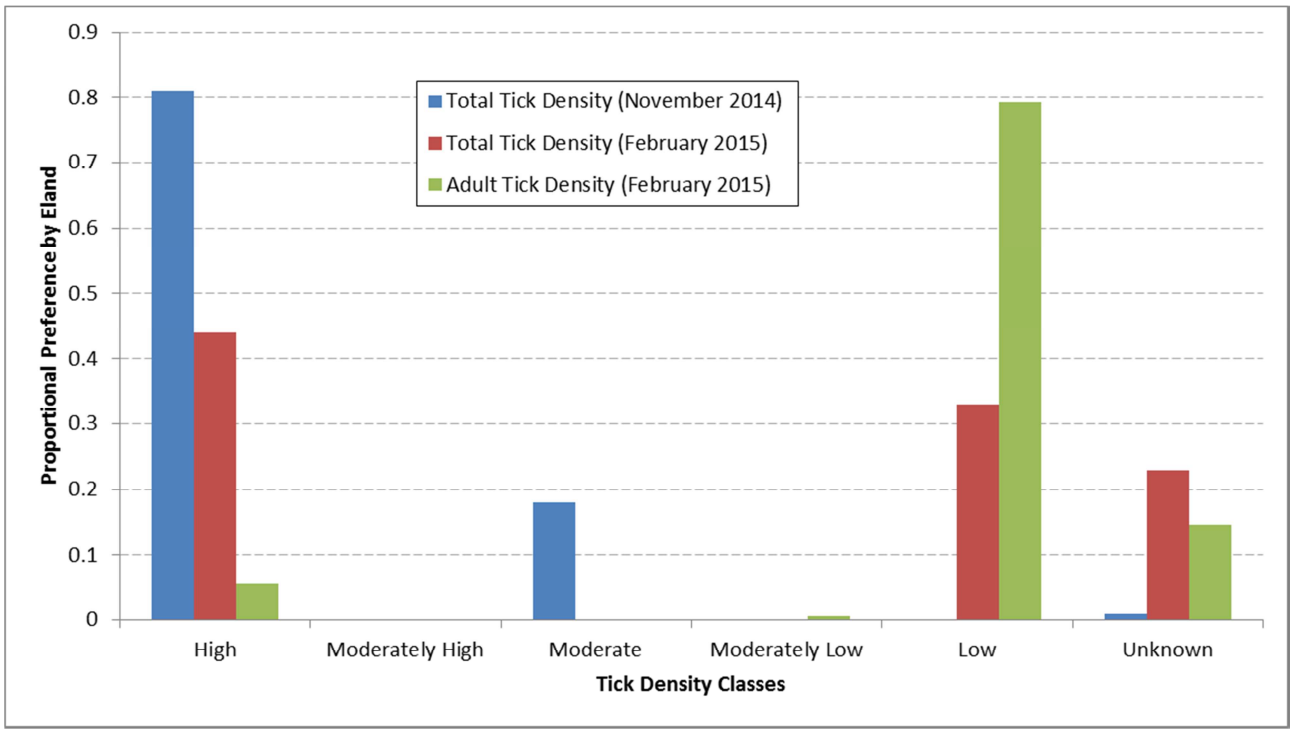


Figure 19: Proportional eland locations per tick abundance class for total and adult tick densities over the respective study periods.

8. DISCUSSION

8.1 The Relationship Between Vegetation Structure and Tick Abundance

The impression gained intuitively during the fieldwork for my study was that there was a clear relationship between tick abundance and vegetation structure type. This difference was statistically significant during both sampling periods, indicating a clear influence exerted by vegetation structure on tick numbers. The results from my study corroborate the findings of Londt and Whitehead (1974); Short *et al.*, (1989a) and Zeiger *et al.*, (1998).

The SUG consistently yielded the lowest tick numbers across both sampling periods. It should be noted that in this instance we are not examining the habitat preferences of ticks. At this scale, it is more likely that ticks are distributed according to the habitat preferences of their hosts. Once discharged from the host, it is the suitability of the habitat for allowing tick survival that determines the tick numbers and developmental stages occurring within that structure type.

Vegetation structure influences the environmental parameters operating within a habitat (Scholes and Archer, 1997; Scholes, 2003), and this is likely to be a key determinant governing tick survival in the SUG. During both sampling periods the majority of the ticks captured in the SUG were larvae and nymphs. Ticks are most vulnerable to desiccation when they are moulting and/ or questing (Walker *et al*., 2003). The smaller bodied the tick, the higher the surface area to volume ratio and the greater the threat of drying out (Lovegrove, 1993). In addition, the exoskeleton is softer and more porous following moulting in the two younger instars than for adult ticks (Walker *et al*., 2003). The SUG consists of a short, herbaceous sward dominated by slender, tufted perennial grasses with a high percentage of bare quartzitic rock surfaces. It is situated topographically in a higher, cooler environment that is more exposed to prevailing winds. The slopes are steep, and the soils coarse-grained, shallow and rocky, factors that promote the rapid removal of rainfall from the ecosystem via surface runoff and the evapotranspiration of water within the limited soil profile (Scholes and Walker, 1993; Schulze *et al*., 2004; Schaezl and Anderson, 2005). The rock surfaces absorb, store and emit greater heat units throughout a 24 hour period than the surrounding vegetation. There is no tree cover to offer resistance to the wind, creating turbulence and lifting the wind away from the sward. The lack of tree cover also removes the shading effect on the underlying sward that would lower daytime temperatures and reduce the evaporative pressure on soil and plants, enhancing soil moisture (Scholes, 2003; Archibald and Scholes, 2007). Tree canopies also capture rainfall, allowing it to drip slowly, or flow down the trunk into the soil beneath (Scholes and Archer, 1997; Scholes, 2003). The capture and removal of kinetic energy from rainfall, and subsequent gentle distribution into the soil beneath the canopy is likely to reduce runoff and promote infiltration (Scholes and Archer, 1997; Scholes, 2003; Archibald and Scholes, 2007), all of which slow down the exit of moisture from the system, promoting moister soil conditions beneath the canopy (Scholes and Archer, 1997; Scholes, 2003). The cumulative effect is a sward micro-climate within the upland grassland types likely to be characterized by: high daytime temperatures (particularly near rock surfaces); high fluctuations in temperature between night and day; limited persistence of water at or near the soil surface even during summer; and consistent and high wind flow. These conditions are likely to promote the desiccation both of plants and organisms within the sward. Tick larvae and nymphs are not able to withstand these conditions (Randolph, 1997; Walker *et al.*, 2003), leading to high mortality and a consequent drop in the abundance of ticks in the SUG areas.

The TUG structure types, characterized by a taller, denser herbaceous layer, flatter topography, sparse rock cover and deeper, heavier soils, contained consistently higher tick

numbers during both sampling periods than the SUG, although the difference was not statistically significant. The stark increase in the sizes of the upper quartile (and sample variance) of the data between November and February indicates an increase in the number and size of larvae nests, which suggests an improvement in larval survival during the late wet season. The TUG structure type is a sink for diffuse runoff from the surrounding SUG slopes (Schulze *et al*., 2004; Fey, 2010). Moisture is retained in the deeper heavier soils for longer periods following rainfall events and the flat topography and dense vegetation cover promote the infiltration of rainfall and runoff (Scholes and Walker, 1993; Schaetzl and Anderson, 2005; Fey, 2010). It is fair to assume that the microclimate within the TUG sward is substantially moister than that of the SUG, particularly in the later season after most of the rain has fallen.

I would have expected there to be significantly more tick larvae in the TUG than the SUG in February, but this was not the case. While using ranked data instead of actual data may have reduced the risk of drawing false positive conclusions (Steele and Torrie, 1980), it may in this case also have diminished the impact of scattered batches of localized aggregates of larvae on the data. Increasing the sample size may be a legitimate way of testing the veracity of these results.

The lowland vegetation structure types, consisting of a taller grass layer and/ or a tree layer of varying height and density, produced significantly greater tick numbers than the SUG in all cases, and TUG in most cases. As expected, the differences were more pronounced in February than in November. The pattern was most prominent in the TLG, ST and TCW, where the height and density of the herbaceous layer of *Hyperthelia dissoluta* serves to break up the desiccating activity of wind through-flow, as well as provide shelter and shade at the base of the grass tufts. This impact is amplified by the presence of a dense tree layer. Their situation in landscape areas that are sheltered, either by their proximity to tall closed woodland or steep slopes, facilitates the dispersal of wind-flow by the tree layer and improves the local soil moisture status (Scholes and Walker, 1993; Archibald *et al*., 2009).

The contribution of soil type to ameliorating micro-climate should not be under-estimated. The ST, TLG and TCW structure types are all situated in the foot-slope and bottomland positions of the terrain, areas that are net accumulators of soil material and rainfall runoff (Schulze *et al*., 2004; Schaezl and Anderson, 2005). They are also geologically underlain by a base-rich, fine-grained material (norite), which translates into deeper, finely-textured soils with a higher water holding capacity (Scholes and Walker, 1993; Schaezl and Anderson, 2005) and nutrient status. These conditions generate high herbaceous biomass production (Tainton, 1999; Uys *et al*., 2004), as evidenced by the dominance of tall, robust

grass species (*H.dissoluta; Hyparrhenia dregeana*). This in turn translates into the production of a sizeable litter layer, which provides ticks with sheltered, moist conditions in which to rehydrate following unsuccessful questing (Medlock *et al.,* 2013). The higher soil water storativity of the deeper soils, coupled with higher moisture status and slower evaporative demand, also creates conditions of higher relative humidity within the sward, resulting in lower tick mortality.

The TOW(S) showed significantly lower tick abundance than the other woodland structure types and the TLG, most likely due to the dominance of short upland grassland species such as *Lodetia simplex*; *Tristachya leucthrix,* the short, fine phenotype of *Themeda triandra* and *Heteropogon contortus*. Unlike the ST and TCW, the trees are widely dispersed, which localizes and dissipates their influence on the prevailing environmental factors (Archibald and Scholes, 2007). The TOW(S) is also characterized by exposed rock at the surface, which is likely to be affecting ground temperature and relative humidity (Archibald and Scholes, 2007). They are situated higher up on the slopes than the other woodland types, where exposure to a greater variation in temperature and wind is higher. The exposure of the sub-canopy to hot, dry air convection is likely to maintain a high evaporative demand even beneath the tree canopies (Scholes and Walker, 1993; Scholes and Archer, 1997), which negates the apparent beneficial influence of microclimate on tick survival and explains why the TOW(S) yielded similar tick abundances to the TUG during both sampling periods. The TOW(T) is situated lower down in the landscape (where wind is less likely to have as important an influence), and has a taller herbaceous layer than TOW(S). This is a possible explanation for the higher tick abundance recorded in the former prior to the onset of the rainy period, when maintaining relative humidity against an overarching hot, dry climate is of amplified importance for tick survival. Interestingly, once substantial rainfall had occurred, there was no difference in tick abundance between the tall open woodland types.

The differences in tick numbers yielded by the various vegetation types differed significantly between the two sampling periods for all vegetation types with the exception of the ST. The evident pattern shows that SUG tick abundance decreased significantly between November and February, while it increased significantly in the TUG and TLG. This suggests that tick survival conditions in grasslands are not solely driven by rainfall, but depend more on an inter-related combination of rainfall, topography and soil type. Each of these influences the nutrient and moisture status of the substrate, the consequent herbaceous vegetation community, the resulting micro-climate within that community, and the associated herbivore community which in turn influences tick occurrence. The combined influence of these environmental factors on tick survival is likely to be non-linear, consisting of certain

thresholds beyond which tick mortality or survival occurs. The ST, the structure type that arguably offers the most sheltered, stable microclimate within the sward, showed no difference in tick numbers between the two sampling periods.

The data analysis certainly suggests a strong pattern between vegetation structure and tick abundance. However, the results are confounded by the direct link between tick abundance and the resource use patterns and availability of hosts (Rizzoli *et al*., 2009; Medlock *et al*., 2013). The more exposed, sourveld areas on the quartzitic slopes provide habitat for fewer large mammal species, simply because they mostly satisfy the resource needs for obligate grazers or concentrate selectors. While eland herds do roam the SUG areas, they are likely to be accompanied only by mountain reedbuck (*Redunca fulvorufula*), klipspringer (*Oreotragus oreotragus*), and jackal (*Canis mesomelas*), animals with small social groupings. Smaller hosts such as mongooses, francolin and hares are likely to avoid these areas because they are exposed and offer little cover against raptors. The rocky habitat also provides ample opportunity for ambush predators such as snakes and caracal (*Felis caracal*). Baboons (*Papio cynocephalus ursinus)* would frequent the upper slopes, although these were not recorded in the SUG areas during field sampling. In contrast, the more stratified structure types lower down in the landscape offer cover and resources for grazers, mixed-feeders and browsers and are hence likely to support a greater variety of host species in higher numbers. Potential tick hosts in these areas are kudu (*Tregalaphus strepsiceros*), zebra (*Equus burchelli*), sable (*Hippotragus niger*), impala (*Aepyceros melampus*), waterbuck (*Kobus ellipsiprymnus*) and monkeys (*Cercopithecus aethips*), all of which are likely to avoid the upland areas. There is also likely to be a greater array of smaller hosts such as several species of mongoose, genet, civet and gamebirds. Baboons may be important tick hosts within the reserve. A strong correlation exists between the number of ticks and the amount of time baboons spend in an area (Brain and Bohrmann, 1992; Akinyi *et al*., 2013). Baboon troops were mostly observed in the TCW and TLG areas during both sampling periods, both of which showed high tick abundances.

Implications of Climate Change

There is already concern among scientists over the potential for ticks to expand in distribution and abundance in response to human-induced climate changes that anticipate higher temperatures (Randolph, 1993; Estrada-Pena, 2008; Medlock *et al.*, 2008; Scharlemann *et al*., 2008; Grey *et al.*, 2009; Gilbert, 2010; Randolph, 2010; James *et al*., 2013; Medlock *et al*., 2013). However, importantly, these studies mostly relate to temperate

northern hemisphere conditions where water and soil moisture are not, unlike low temperatures, limiting ecological factors. In contrast, in African savannas water and soil moisture are, unlike temperature, the important limiting resources (Scholes and Walker, 1993; Scholes and Archer, 1997; Archibald and Scholes, 2007).

Ultimately the consequences of climate change on tick abundance are difficult to predict due to the non-linear complexity of the interrelated ecological relationships. Certainly there is evidence of woody species expansion into grassland areas (O' Connor and Berdenkamp; 1997; Mucina and Rutherford, 2006), and bush encroachment is a well-documented phenomenon in savannas (Bond and Midgely, 2002; Sankaran *et al*., 2005; Ward, 2005; Wiegand *et al*., 2006). Both phenomena can be linked to climate change. My results would suggest that tick abundance will increase in both situations, presupposing that the sub-canopy microclimate will enhance tick off-host survival. This mirrors the conclusions drawn by the northern-hemisphere studies.

However, low relative humidity and soil moisture have been identified as key factors driving tick mortality, particularly in the younger life stages. Higher air temperatures, drier atmospheric conditions and a drier, more erratic rainfall regime may negate the microclimatic advantages provided by a tall sward and tree canopy cover and push the in-sward environmental conditions towards those more applicable to the upland grasslands and TOW(S). The reduction in herbaceous primary production could affect grass tuft vigour and density, and diminish the litter layer and the succor it provides to ticks. Increased evapotranspiration and evaporation could reduce microclimate relative humidity, increasing desiccation among questing ticks and impeding their ability to rehydrate. My results indicate that this would be detrimental to tick abundance. Hence the anticipated changes to regional climate are, based on the insight I have gained from this study, likely to result in a lower tick abundance in semi-arid rangeland ecosystems (such as those found in KMR) as tick off-host mortality increases.

A feasible scenario could also be a shift in tick species composition, with more drought resistant tick genera becoming dominant. An increase in 1-host and 2-host tick species, where the time spent off the host and exposed to the elements is minimized, might be expected and this could maintain tick abundance, provided that the availability of hosts remained unchanged.

Management Implications

My results suggest that open rangelands with a shorter sward support smaller tick populations than denser, more sheltered structure types such as tall, lowland grasslands, shrublands and closed to mixed woodlands. A prominent feature of small nature reserves and game farms is the absence of animals capable of physically manipulating vegetation structure across the local landscape. For example, KMR does not have bulk grazers such as white rhino (*Ceratotherium simum*) and buffalo (*Syncerus cafer*) herds that trample and graze as they forage, resulting in a shorter, more open sward in areas dominated by taller grass species. The presence of these animals could substantially shorten the herbaceous layer in the TUG, TLG, ST and TOW(T) structure types, allowing air to circulate and dry the microclimate out, creating less favourable conditions for ticks. New grass growth is more nutritious than older growth (Tainton, 1999; Uys, 2006), and bulk grazers tend to rotate through previously grazed lands utilizing the new growth that accumulates during the grazing interval. Sward height through repeated grazing, and the suppressive effect this has on tick numbers, is therefore maintained (unlike fire, which has a once-off effect). The ecological influence of native bulk grazers can be simulated by substituting cattle for buffalo, and using these to control the height of the sward. This carries the added advantages that cattle movement is easier to manage; there is an additional income stream from beef production; and it is possible to dip cattle with acaricide and in so doing remove ticks from the system.

Large browsers such as black rhino (*Diceros bicornis*) and, in particular, elephant (*Loxodonta africana*) create more open savanna vegetation by trampling and destroying trees, which favours and stimulates production in the grass layer (Stuart-Hill *et al*., 1987; Scholes and Walker, 1993; Scholes and Archer, 1997). This also ensures that replacement tree seedlings are maintained within the fire trap (Bond and Keeley, 2005), and are able to be killed or inhibited by subsequent fire events. This, however, also can have a negative impact as the sward may become dominated by short shrubs.

Should tick infestation become a problem, a possible management option would be to replicate the effects of these large herbivores mechanically, in so doing physically and strategically manipulating vegetation structure to create areas that are less hospitable to ticks. This includes physically removing trees and shrubs to open up woodland and shrubland areas, or mowing taller grassland swards to maintain them at a shorter height. These measures, however, substantially increase the operating costs of the concern.

Fire is also an effective manipulator of vegetation structure (Bond and Keeley, 2005; Bond, 2008). Fires themselves do not affect tick populations because they are single events,

and the burned area is rapidly recolonized once the new grass growth attracts hosts (Zeiger *et al.*, 1998). However a long-term, strategically managed and implemented fire regime is an effective tool in maintaining or creating the desired vegetation structure types, which could then influence tick abundance. While fires are effective at controlling tree recruitment (Bond and Keeley, 2005), they occur at intervals that are less effective at controlling sward height. As a mechanism for controlling tick populations, fire is likely to be most effective when combined with the activity of large herbivores or mechanical operations.

8.2 The Influence of Vegetation Structure on Tick Development During the Sampling Periods

The overwhelming majority of the ticks trapped during the two sampling periods where larvae. The pattern of their occurrence, however, was distinctly different with their numbers in February represented by few large aggregations rather than the consistent numbers encountered during November. Few adult ticks were encountered during November, while nymphs were virtually absent from the February sampling period.

The SUG had the lowest numbers of all tick life stages across the study period. A possible reason for this is more malign conditions for tick survival prevailing in the SUG areas, leading to increased tick mortality as discussed in the previous section. The paucity of hosts in this structure type also means that ticks are likely to wait for long periods before intercepting a suitable host, leading to increased mortality as questing ticks run out of reserves (Zieger *et al*., 1995; Ruiz-Fons *et al*, 2012; Medlock *et al*., 2013).

The highest nymph numbers were recorded in November. Over this time most ungulates seek shade in more sheltered vegetation types during the hot daytime hours. Engorged nymphs detach mainly between 12h00 and 18h00 (Minshull, 1982), and would drop into the shaded areas, moult into the adult stage and begin questing. This may partially explain the high numbers of adult ticks found in the ST and TCW structure types during the later sampling period. Tick larvae and nymphs are smaller bodied and more prone to desiccation than adults (Walker *et al*., 2003; Medlock *et al*., 2013). The higher larvae and nymph mortality occurring in the upland grassland types would explain the dearth of adults in these types. The ST and TCW types produce more sheltered, benign microclimatic conditions, resulting in higher nymph survival, which translates into the high numbers of adult ticks evident in these structure types.

Tick larvae tend to be more abundant during the winter months and are prevalent in higher numbers in open grasslands (Zieger *et al*., 1995). Ungulates do not need to regulate their temperature during winter, and hence spend a greater part of the day utilizing open areas. Engorged larvae detach from hosts mainly between 10h00 and 14h00 (Minshall, 1982), dropping into the open areas before moulting to form nymphs. This may explain why the TLG and ST, which incidentally provide greater forage potential to mixed feeders, had the highest numbers of nymphs in November.

These patterns of ungulate behavior correspond with the eland location data obtained for this project. During the late winter and early summer months the eland were concentrated in the TLG structure type. Other mammals such as kudu, baboons and waterbuck were also observed congregating in these areas. It stands to reason that a higher number of engorged adult ticks would drop off into this structure type during this time. This may explain the exceptionally high larvae numbers recorded in the TLG during the February sampling period.

The physical structure of the vegetation may also influence animal movement. This affects the areas where ticks are deposited, but more importantly affects the frequency and reliability of ticks intercepting hosts. For example, the ST structure type consists of long grass interspersed with densely scattered shrubs. Movement is confined to the gaps between the shrubs, which serves to concentrate animal movement. Ticks dropped in this structure type are sheltered from desiccation, and are also able to reliably find hosts to complete the next phase of their life cycle. In contrast, eland in the SUG are free to roam and disperse in a diffuse pattern which must substantially reduce the chances of questing ticks intercepting them.

Peak calving for eland is at the end of the dry season, September to October in South Africa (Apps, 1996). Assuming calving period is related to seasonal forage availability (McNaughton, 1990; Pappas, 2002) it is feasible that calving may have been delayed until later in the season in KMR due to the lateness of the rains. Eland calves are hidden for the first two weeks of their lives, before joining the herd (Apps, 1996). The calves are usually hidden in areas that provide cover from predators, such as tall, dense stands of grass and shrublands. The period that calves are in hiding corresponds with the period of low tick nymph numbers and absence of adult ticks in the ST, TLG and TCW structure types, areas where eland calves are most likely to be hidden. Later in the season, following the onset of the rains, eland family units congregate into large herds that, in the case of KMR, move into the open upland grasslands. The calves congregate into nursery herds within these large herds (Skinner and Smithers, 1990; Skinner *et al*., 1974; Apps, 1996). This period corresponds with the virtual absence of tick adults and nymphs from the SUG and TUG areas. The results of

this study certainly suggest that the prevailing eland movement patterns expose their calves to lower potential infestation from nymph and adult ticks, the life stages that would arguably have the greatest physical impact on them.

8.3 The Influence of Rainfall Season on Diurnal Tick Activity

The pooled data revealed no difference in tick activity between the different times of the day. Overall diurnal tick activity patterns were also the same for both the November and February sampling periods. Spicket *et al*., (1991) noted a similar outcome.

It was anticipated that the upland grassland types would show greater tick activity during the cooler, more humid times of the day while the more sheltered, denser structure types such as the ST and TCW would show more constant levels of activity throughout the day because they would be less influenced by temperature and wind flow. There was, however, little evidence of a clear pattern linking structural components to increased activity at certain times of the day. A pattern that is evident, however, is an evening out of tick activity between the diurnal time periods from November to February. In November there were differences in activity in half of the structure types, while in February tick activity during the morning, midday and afternoon periods was the same for almost all structure types. It is possible that the improved environmental conditions brought about by rainfall, namely higher relative humidity and more sheltered micro-climate conditions resulting from new leaf-growth, enable the ticks to spend longer questing before they need to descend the grass to rehydrate. They may also be able to rehydrate at any time of the day, as opposed to only at night during the drier season, and so do not need to co-ordinate questing according to specific times.

In general, the SUG showed significantly lower levels of tick activity across all three time periods than the other structure types for both sampling periods. The TUG grassland also showed lower tick activity in the morning and afternoon than in the ST and TCW structure types. These conclusions may, however, be compromised in that the method of comparison of activity is based on tick abundance, which is considerably lower for the SUG. In hindsight, I should have compared proportional tick abundance across the three diurnal time periods between the structure types as this would have indicated when the ticks that are present in the transect at the time of sampling are most active.

There was no difference in diurnal tick activity pattern between November and February in the denser lowland structure types, indicating that micro-climatic conditions are stable enough to support questing at any time of the day. The suppressed morning and

afternoon activity in February in the upland grassland types is contrary to expectations, and difficult to explain without more accurate micro-climate data. What is evident is that ticks seem more likely to co-ordinate their questing behavior according to prevailing environmental conditions in the sward rather than to host activity.

In hindsight the data collected during my study is probably insufficient to reach reliable conclusions regarding tick questing activity. This was a secondary objective of the study, in truth a means of seeking to maximize the information obtained from the data collection. To answer the question fully would require more intensive data collection, and a study designed to address the specific question. There is little evidence in the literature to suggest that ticks are more active during the day than during the night. Nocturnal climatic conditions during summer are likely to be more benign for questing ticks, and hence any investigation into tick activity would have to include this period. However, if ticks are more reliant on nocturnal conditions to rehydrate, they may be less likely to risk dehydration by increasing their nocturnal activity. Tick sampling should be carried out in each structure type at specified intervals throughout the day (and night), for example at half-hour intervals. These may be replicated spatially, with three drags per sample, and/ or temporally with repeated sampling throughout a specified time period. This would generate more robust data, facilitating the drawing of more reliable conclusions.

8.4 The Potential for Tick Abundance to Influence Eland Use of Space

Eland movement within the reserve during the sampling periods showed two distinct patterns. The first was behavioural, with all of the eland congregating during the later wet season to form one herd. The second is spatial, with eland spending most of their time in the lowlands and bottomlands of the central valley during November, and being confined exclusively to the uplands during the February sampling period. There is a clear relationship between eland location and vegetation structure type during both sampling periods.

There are a number of possible explanations for this behaviour. Arguably the overriding influence is forage quality. The mesic grasslands of the upland areas are likely to be “sourveld”, which is defined as rangeland that is able to support animal production for 6 months of the year (Ellery *et al*., 1995; Tainton, 1999). Sourveld grasses are only palatable during the summer months. While the main determinant is high rainfall which drives the leaching of nutrients from the soil profile (Cadman *et al*., 2013), poor nutrient status of the soil may also limit forage palatability (Ellery *et al*., 1995). In winter sourveld grasses

withdraw the nutrients from their foliage, commencing in autumn, resulting in the leaves being unpalatable during winter (Tainton, 1999; Cadman *et al.*, 2013).

The grazing in the low-lying TLG areas, with a higher soil base status (Ellery *et al*., 1995), is likely to be "mixed-veld" (able to support animal production for 9 months) or "sweetveld" (able to support animal production for the entire year) (Tainton, 1999; Cadman *et al.*, 2013). These veld types tend to maintain their palatability through winter (Ellery *et al*., 1995). This allows eland to graze selectively in the bottomlands during winter, to the point where 31% of the dry season diet is grass (*T.leucothrix*) (D'Ammando *et al*., 2014). As predominantly browsers, eland are also in a better position to exploit shrubs and broadleaved plants over a smaller area in the central valley. The shift by eland to the uplands follows the onset of the summer rains. This coincides with an improvement in forage quality as previously dormant sourveld grasses become more palatable with the commencement of seasonal growth (Ellery *et al*., 1995; Tainton, 1999). This pattern of movement is consistent over more than a single season, and is not influenced by the occurrence of late season fires.

The key feature of this movement pattern is that it enables eland to avoid adult ticks because they are able to exploit forage that is less palatable at other times of the year. Eland were not influenced by total tick abundance whatsoever during either sampling period. Total tick numbers consisted mostly of larvae and nymphs. Eland did, however, clearly select areas in February with low adult tick abundance, and avoided areas of high adult tick abundance, specifically the ST and TCW. The pattern was non-existent in November because there were so few adult ticks present. The smaller tick life stages may not be large enough to impact on the animals comfort levels. Adult ticks however, particularly if they occur in high numbers, are able to cause a behavioural change in animals. Examples are easily observed and include: mutual grooming in ungulates (Mooring *et al*., 2004); mud wallowing by rhino, buffalo and warthog, and subsequent rubbing of the hide against stumps (Estes, 1999; Apps, 1996); eland rubbing their inner thighs against thorny saplings in an effort to remove ticks (personal observation during this study); and ungulates accommodating oxpeckers. There is hence evidence suggesting that animals are able to link the presence of adult ticks with extreme discomfort, and alter their behavior to manage this.

In mid-to-late summer forage quality in the upland grasslands may be sufficiently palatable for eland to become temporary facultative grazers. Eland move out of the valley and congregate, with the season's calves, in the uplands where the challenge from adult ticks is minimal. Animals are able to move in order to avoid areas where the predation risk is highest (such as impala congregating in open areas at night) (Scheel, 1993; Ogutu and Owen-Smith, 2005; Valeix *et al*., 2009), and congregate in areas where there is some form of positive

feedback (salt-licks; sodic sites). It is not inconceivable that animals will also be able to associate certain habitat types with high tick loads at certain times of the year. Access to an alternative source of suitably high quality forage, other than browse, allows eland to prioritise physical comfort over optimizing diet quality. Eland are supposedly independent of water because of the high moisture content of their browse diet (Watson and Owen-Smith, 2000). A change in diet to grass forage may cause them to become temporarily more dependent on water, of which there is an ample supply in the wetland on the high plateau. With the onset of autumn, when the forage quality in the upland areas decreases as the grass cures, and when adult tick numbers ostensibly decline and larvae become more numerous (Zieger *et al*., 1995), eland are able to move back into the valley to exploit the seasonally higher forage quality with a lower risk of infestation from adult ticks.

There are several other possible explanations for these movement patterns. The upland areas are exposed to prevailing winds, which may cool the animals down. One would have thought, however, with February traditionally being one of the hottest months, if thermoregulation was a priority then more of the eland locations would be in areas with tree cover.

The influence of innate behavior in animals should not be underestimated. The movement of eland into the uplands during the period when calves are most likely to be at their most vulnerable may also be an inherited anti-predator strategy, even though predators are absent from the reserve. Open rangelands provide little cover for predators to stalk from, and the improved visibility also allows animals to detect predators more easily. The congregation of family groups into larger herds disperses the risk of predation among the larger population. There is the added protection for calves potentially offered by many adults against predators, and there are a greater number of eyes and ears alert to potential threats.

9. CONCLUSIONS

The study has illustrated that the hypothesis for objective 1 is correct. Tick numbers are influenced by vegetation structure, and are higher in the more sheltered, denser structure types. The short, open mesic grasslands on the exposed quartzite ridges contained the lowest numbers of ticks for both sampling periods. There is evidence suggesting that tick survival is not solely driven by rainfall, but rather a combination of interrelated factors including rainfall. These are likely to be non-linear. The sheltered, dense ST structure type showed no difference in tick abundance between the two periods, in contrast to the more open, exposed

structure types. Tick abundance is reliant on the availability of hosts. Based on the insight gained from this study, tick populations are expected to decline in response to the anticipated change in local climatic conditions associated with global climate change, unless more drought resistant tick species become dominant. The relationship observed between tick abundance and vegetation structure provides a rationale for using various management interventions to physically manipulate vegetation structure in order to control tick populations.

The results indicate that the hypothesis that adult ticks are more prominent in November was false. Adults are virtually absent from the landscape in November, and are more prominent during February. This outcome corresponds with several other studies. The larval and nymph stages dominate the drier months, possibly indicating that although atmospheric conditions are drier at this time, the lower temperatures and frequent dews provide more benign conditions among the leaf litter and grass tuft bases. Evidence suggests that the hypothesis that adult ticks occur in higher numbers in the sheltered structure types is correct, and that the rationale behind this is sound. However, the patterns of occurrence of the various life stages are also linked to host behavior. Most importantly, the results suggest that the spatial characteristics of eland calving behavior, based on existing regional data, coincide with patterns of low adult tick abundance.

There were no differences in the overall pattern of tick activity between the morning, midday and afternoon times, and between the November and February sampling periods. The data were deemed insufficient to draw any further conclusions. The method of analysis was flawed, and more meaningful results may be obtained by estimating tick activity according to the proportion of ticks caught across the time periods for each sample, rather than tick numbers.

Based on the outcome of the study, the hypothesis for objective 4 must be rejected. Eland give no consideration whatsoever to *total* tick abundance, and the results suggest that some other factor, such as forage selection, is an overriding priority governing eland location during both sampling periods. However, a pattern is certainly evident that suggests that eland do select areas of low *adult* tick abundance, and avoid areas of high *adult* tick abundance during the mid-to-late summer period. The improvement in forage quality in the upland grasslands associated with the summer rainfall season, and their proven inclination to include a substantial portion of grass in their diet, provides them with the opportunity to prioritise physical comfort (for themselves and their calves) over diet quality. There is ample, and easily observable, evidence that tick infestation exerts a large enough pressure to cause animals to modify their behavior. Animals are also able to associate certain characteristics of

the habitat with positive or negative feedbacks. With this in mind, and in view of the patterns identified by this study, it is certainly plausible that the potential for *adult* tick infestation can be a driver for the modification of resource use by eland. The observed patterns are compatible with a reduction in the risk of potential exposure of eland calves to *adult* ticks.

The findings link both the influence of vegetation structure on tick mortality, and the potential and plausible influence of adult tick abundance on animal movement. Small nature reserves and game farms generally lack two critical components controlling adult tick numbers, namely oxpeckers and large, heavy herbivores. Artificially recreating their ecological uses through applied, management interventions may pay dividends commercially by limiting the adverse effects of ticks on animals, and allowing better resource use by animals thereby improving growth and birth rates.

10. DIRECTION FOR FUTURE RESEARCH

The drawback in conducting a field investigation such as this is that it is physically impossible to create individual treatments where non-target hosts are removed and tick abundance levels are accurately controlled. The direct comparison of target animal response to tick abundance is impossible. However, it is worthy of research. While there is literature describing animal movement in response to food availability, thermoregulation, predation, reproduction and various other factors, there is little evidence that tick infestation may be a high enough priority to modify animal movement. To my knowledge it is new research. The most appropriate means of investigating this in the field is by undertaking a series of studies, each of which fills another piece of the puzzle. My study has succeeded in identifying and exposing certain patterns that may become more robust with additional research.

The correlation between microclimate and tick abundance would be more lucid if temperature and relative humidity were measured in each vegetation structure type. This would assign greater confidence to the rationale behind many of the conclusions I have drawn (or refute them legitimately). An attempt was made to measure these parameters to provide a foundation against which to discuss the results of this study, but in hindsight the data would have been fundamentally flawed because there was only one data-logger per structure type. The data should have at least 3 replications, translating into 21 data-loggers distributed evenly across the structure types. I suspect that the mini-Stevenson's screens I constructed to protect the data-loggers were also incorrect in that they did not allow sufficient air circulation, which distorted the results. The reason I did not include these data in the research

discussion is that I lost half of the data-loggers due to a combination of theft and baboon-vandalism.

My research illustrated that ticks and nymphs do not influence eland movement, but it is plausible that adult ticks could. I would concentrate future research on adult tick abundance only. A key constituent missing from this study is the abundance and distribution of the large exophilic ticks of the *Amblyomma* and *Hyalomma* genera. These track hosts by following the carbon dioxide concentration (Walker *et al*., 2003) and, because of their size, may exert the greatest pressure and discomfort on ungulate hosts. It would be important to include these in future research.

The assumptions I have made regarding forage quality during the respective sampling periods are sound, and based on rigorous, peer-reviewed, published literature. They are still, however, assumptions. Additional research should include the in-field identification of the seasonal diet (to the species level) of eland at KMR for an entire year. This could be combined with the laboratory analysis of the dominant species contributing to seasonal diet in order to empirically measure forage quality, and crude protein in particular.

The research into the complex relationships between ticks, vegetation and animals may have practical applications. Once the ecological processes are better understood, research could be expanded into the effects of management interventions such as mowing or bush clearance on these relationships, and whether these can be manipulated to achieve a set of specific objectives.

Finally, I would extend this study across the entire year to examine tick abundance and eland movement patterns across all four seasons. It would be interesting to see whether the patterns I have identified are consistent throughout the year. This could take the form of an ongoing monitoring programme, exploring the response of ticks and their hosts to varying climatic conditions.

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12. APPENDIX

The following tables are referenced in the text.

Table I: Results of Dunn's post-hoc tests, showing the statistical significance of the relationship between tick larvae and vegetation structure type. The two-sided Bonferrini z-values are: α (0.05) = 3.038; α (0.01) = 3.494; n = 7; no. of pairwise comparisons = 21.

Tick Larvae	SUG	TUG	TLG	ST	TCW	TOW (S)	TOW(T)
November 2014							
SUG	-						
TUG	1.872	-					
TLG	4.811**	2.939	-				
ST	4.306**	2.434	0.505	-			
TCW	7.592**	5.72**	2.781	3.286*	-		
TOW (S)	1.949	0.077	2.862	2.357	5.643**	-	
TOW(T)	5.485**	3.613**	0.674	1.179	2.107	3.536**	-
February 2015							
SUG	-						
TUG	2.470	-					
TLG	7.572**	5.102**	-				
ST	3.634**	1.164	3.938**	-			
TCW	2.616	0.146	4.957**	1.019	-		
TOW (S)	3.384*	0.914	4.188**	0.250	0.769	-	
TOW(T)	4.641**	2.170	2.932	1.006	2.025	1.256	-

* = p (0.05)

** = P (0.01)

Table II: Results of Dunn's post-hoc tests, showing the statistical significance of the relationship between tick nymphs and vegetation structure type. The two-sided Bonferrini z-values are: α (0.05) = 3.038; α (0.01) = 3.494; n = 7; no. of pairwise comparisons = 21.

Tick Nymphs	SUG	TUG	TLG	ST	TCW	TOW (S)	TOW(T)
November 2014							
SUG	-						
TUG	3.799**	-					
TLG	6.351**	2.552	-				
ST	5.774**	1.975	0.577	-			
TCW	4.654**	0.856	1.697	1.119	-		
TOW (S)	2.792	1.006	3.559**	2.981	1.862	-	
TOW(T)	4.004**	0.205	2.347	1.770	0.651	1.211	-
February 2015							
SUG	-						
TUG	0.235	-					
TLG	0.9400	0.705	-				
ST	1.4100	1.175	0.470	-			
TCW	2.351	2.116	1.410	0.940	-		
TOW (S)	0.940	0.705	0.000	0.470	1.410	-	
TOW(T)	0.235	0.000	0.705	1.175	2.116	0.705	-

* = p (0.05)

** = P (0.01)

Table III: Results of Dunn's post-hoc tests, showing the statistical significance of the relationship between tick adults and vegetation structure type. The two-sided Bonferrini z-values are: α (0.05) = 3.038; α (0.01) = 3.494; n = 7; no. of pairwise comparisons = 21.

Adult Ticks	SUG	TUG	TLG	ST	TCW	TOW (S)	TOW(T)
November 2014							
SUG	-						
TUG	0.000	-					
TLG	0.000	0.000	-				
ST	0.711	0.711	0.711	-			
TCW	0.233	0.233	0.233	0.479	-		
TOW (S)	0.233	0.233	0.233	0.479	0.000	-	-
TOW(T)	1.409	1.409	1.409	0.698	1.177	1.177	
February 2015							
SUG	-						
TUG	0.287	-					
TLG	1.215	1.503	-				
ST	6.229**	6.516**	5.014**	-			
TCW	6.319**	6.606**	5.103**	0.090	-		
TOW (S)	1.741	2.029	0.526	4.488**	4.577**	-	
TOW(T)	0.299	0.586	0.917	5.931**	6.02**	1.443	-

* = p (0.05)

** = P (0.01)

Table IV: Results of the Dunn post-hoc tests, showing the statistical significance of the relationship between morning tick activity and vegetation structure type. The two-sided Bonferrini z-values are: α (0.05) = 3.038; α (0.01) = 3.494; n = 7; no. of pairwise comparisons = 21.

Morning	SUG	TUG	TLG	ST	TCW	TOW (S)	TOW(T)
November 2014							
SUG	-						
TUG	1.903	-					
TLG	4.546**	2.642	-				
ST	4.128**	2.225	0.418	-			
TCW	4.931**	3.028	0.386	0.804	-		
TOW (S)	1.305	0.598	3.24*	2.822	3.626**	-	
TOW(T)	3.935**	2.032	0.611	0.193	0.997	2.630	-
February 2015							
SUG	-						
TUG	0.720	-					
TLG	4.61**	3.89**	-				
ST	4.089**	3.369*	0.521	-			
TCW	2.604	1.884	2.006	1.485	-		
TOW (S)	1.138	0.418	3.472*	2.951	1.466	-	
TOW(T)	3.581**	2.861	1.029	0.508	0.977	2.443	-

* = p (0.05)

** = P (0.01)

Table V: Results of the Dunn post-hoc tests, showing the statistical significance of the relationship between midday tick activity and vegetation structure type. The two-sided Bonferrini z-values are: α (0.05) = 3.038; α (0.01) = 3.494; n = 7; no. of pairwise comparisons = 21.

Midday	SUG	TUG	TLG	ST	TCW	TOW (S)	TOW(T)
November 2014							
SUG	-						
TUG	0.405	-					
TLG	3.62**	3.215*	-				
ST	3.922**	3.517**	0.302	-			
TCW	4.417**	4.012**	0.797	0.495	-		
TOW (S)	3.53**	3.125*	0.090	0.392	0.887	-	
TOW(T)	3.009	2.604	0.611	0.913	1.408	0.521	-
February 2015							
SUG	-						
TUG	1.916	-					
TLG	4.436**	2.520	-				
ST	3.575**	1.659	0.862	-			
TCW	2.276	0.360	2.160	1.299	-		
TOW (S)	2.713	0.797	1.723	0.862	0.437	-	
TOW(T)	1.376	0.540	3.06*	2.199	0.900	1.337	-

* = p (0.05)

** = P (0.01)

Table VI: Results of the Dunn post-hoc tests, showing the statistical significance of the relationship between afternoon tick activity and vegetation structure type. The two-sided Bonferroni z-values are: α (0.05) = 3.038; α (0.01) = 3.494; n = 7; no. of pairwise comparisons = 21.

Afternoon	SUG	TUG	TLG	ST	TCW	TOW (S)	TOW(T)
November 2014							
SUG	-						
TUG	2.405	-					
TLG	3.208*	0.804	-				
ST	2.424	0.019	0.784	-			
TCW	4.365**	1.961	1.157	1.942	-		
TOW (S)	0.077	2.327	3.131*	2.347	4.288**	-	
TOW(T)	4.128**	1.723	0.919	1.704	0.238	4.05**	-
February 2015							
SUG	-						
TUG	1.254	-					
TLG	4.816**	3.562**	-				
ST	4.571**	3.318*	0.244	-			
TCW	3.311*	2.057	1.504	1.260	-		
TOW (S)	2.102	0.849	2.713	2.469	1.209	-	
TOW(T)	2.308	1.054	2.507	2.263	1.003	0.206	-

* = p (0.05)

** = P (0.01)

Table VII: Proportional availability and locations logged for eland across vegetation structure types during November 2014. The data consists of the collective locations for four collared eland cows. Bonferroni confidence intervals (determined at the 95% level) were used to determine eland selection and avoidance of structure types.

Vegetation Structure Type	Total hectares	Proportion of total hectarage	Observed Number of Eland GPS Locations	Expected Number of Eland GPS Locations	Proportion Observed Locations per Structure Type	Expected Proportion per Structure Type	Confidence Interval on Proportion of Locations	
SUG	2074.5	0.452	342	978.73	0.158	0.452	$0.137 \leq P_0 \leq 0.179$*	-
TUG	857.7	0.187	327	404.66	0.151	0.187	$0.130 \leq P_0 \leq 0.172$*	-
TLG	72.8	0.016	411	34.35	0.190	0.016	$0.167 \leq P_0 \leq 0.212$*	+
ST	43.2	0.009	4	20.38	0.002	0.009	$-0.001 \leq P_0 \leq 0.004$*	-
TCW	639.9	0.139	254	301.90	0.117	0.139	$0.099 \leq P_0 \leq 0.136$*	-
TOW(T)	434.0	0.095	343	204.76	0.158	0.095	$0.137 \leq P_0 \leq 0.180$*	+
TOW(S)	468.9	0.102	485	221.22	0.224	0.102	$0.20 \leq P_0 \leq 0.248$*	+
Total	**4591.0**	**1.000**	**2166**	**2166**	**1.000**	**1.000**		

***** **Significant at $p \leq 0.05$**

+ **Selection for Vegetation Structure Type**

- **Avoidance of Vegetation Structure Type**

Table VIII: Proportional availability and locations logged for eland across vegetation structure types during February 2015. The data consists of the collective locations for four collared eland cows. Bonferroni confidence intervals (determined at the 95% level) were used to determine eland selection and avoidance of structure types.

Vegetation Structure Type	Total hectares	Proportion of total hectarage	Observed Number of Eland GPS Locations	Expected Number of Eland GPS Locations	Proportion Observed Locations per Structure Type	Expected Proportion per Structure Type	Confidence Interval on Proportion of Locations	
SUG	2074.5	0.452	1354	1528	0.464	0.452	0.439 ≤ P0≤ 0.489	
TUG	857.7	0.187	1292	632	0.442	0.187	0.418 ≤ P0≤ 0.467*	+
TLG	72.8	0.016	1	54	0.000	0.016	-0.001 ≤ P0≤ 0.001*	-
ST	43.2	0.009	0	32	0.000	0.009	0.000 ≤ P0≤ 0.000*	-
TCW	639.9	0.139	194	471	0.066	0.139	0.054 ≤ P0≤ 0.079*	-
TOW(T)	434.0	0.095	60	320	0.021	0.095	0.013 ≤ P0≤ 0.028*	-
TOW(S)	468.9	0.102	19	345	0.007	0.102	0.002 ≤ P0≤ 0.011*	-
Total	**4591.0**	**1.000**	**2920**	**3381**	**1.000**	**1.000**		

***** **Significant at p ≤ 0.05**

+ **Selection for Vegetation Structure Type**

- **Avoidance of Vegetation Structure Type**

Table IX: Proportional availability and locations logged for eland across vegetation structure types during the November 2013. The data are from a single collared eland cow. Bonferroni confidence intervals (determined at the 95% level) were used to determine eland selection and avoidance of structure types.

Vegetation Structure Type	Total hectares	Proportion of total hectarage	Observed Number of Eland GPS Locations	Expected Number of Eland GPS Locations	Proportion Observed Locations per Structure Type	Expected Proportion per Structure Type	Confidence Interval on Proportion of Locations	
SUG	2074.5	0.452	2	42	0.022	0.452	-0.019 ≤ P0≤ 0.063*	-
TUG	857.7	0.187	17	17	0.185	0.187	0.076 ≤ P0≤ 0.294	
TLG	72.8	0.016	18	1	0.196	0.016	0.084 ≤ P0≤ 0.307*	+
ST	43.2	0.009	0	1	0.000	0.009	0.000 ≤ P0≤ 0.000	
TCW	639.9	0.139	7	13	0.076	0.139	0.001 ≤ P0≤ 0.151	
TOW(T)	434.0	0.095	39	9	0.424	0.095	0.285 ≤ P0≤ 0.563*	+
TOW(S)	468.9	0.102	9	9	0.098	0.102	0.014 ≤ P0≤ 0.181	
Total	**4591.0**	**1.000**	**2920**	**3381**	**1.000**	**1.000**		

***** **Significant at p ≤ 0.05**

+ **Selection for Vegetation Structure Type**

- **Avoidance of Vegetation Structure Type**

Table X: Proportional availability and locations logged for eland across vegetation structure types during the February 2014. The data are from a single collared eland cow. Bonferroni confidence intervals (determined at the 95% level) were used to determine eland selection and avoidance of structure types.

Vegetation Structure Type	Total hectares	Proportion of total hectarage	Observed Number of Eland GPS Locations	Expected Number of Eland GPS Locations	Proportion Observed Locations per Structure Type	Expected Proportion per Structure Type	Confidence Interval on Proportion of Locations	
SUG	2074.5	0.452	147	126	0.521	0.452	0.441 ≤ P0≤ 0.602	
TUG	857.7	0.187	115	52	0.408	0.187	0.329 ≤ P0≤ 0.487*	+
TLG	72.8	0.016	0	4	0.000	0.016	0.000 ≤ P0≤ 0.000*	-
ST	43.2	0.009	1	3	0.004	0.009	-0.006 ≤ P0≤ 0.013	
TCW	639.9	0.139	16	39	0.057	0.139	0.020 ≤ P0≤ 0.094*	-
TOW(T)	434.0	0.095	3	26	0.011	0.095	-0.006 ≤ P0≤ 0.027*	-
TOW(S)	468.9	0.102	0	29	0.000	0.102	0.000 ≤ P0≤ 0.000*	-
Total	**4591.0**	**1.000**	**2920**	**3381**	**1.000**	**1.000**		

***** **Significant at p ≤ 0.05**

+ **Selection for Vegetation Structure Type**

- **Avoidance of Vegetation Structure Type**

Table XI: Proportional availability and locations logged for eland across areas classified according to total tick abundance during November 2014. The data consists of the collective locations for four collared eland cows. Bonferroni confidence intervals (determined at the 95% level) were used to determine eland selection and avoidance according to tick abundance.

Total Tick Abundance	Total hectares	Proportion of total hectarage	Observed Number of Eland GPS Locations	Expected Number of Eland GPS Locations	Proportion Observed Locations per Abundance Class	Expected Proportion per Abundance Class	Confidence Interval on Proportion of Locations	
High	2516.70	0.5416	1627	1089.65	0.809	0.542	0.786 ≤ P0≤ 0.831*	+
Moderately High	0.00	0.0000	0	0.00	0.000	0.000	0.00 ≤ P0≤ 0.00	
Moderate	2074.58	0.4464	364	898.23	0.181	0.446	0.159 ≤ P0≤ 0.203*	-
Moderately Low	0.00	0.0000	0	0.00	0.000	0.000	0.00 ≤ P0≤ 0.00	
Low	0.00	0.0000	0	0.00	0.000	0.000	0.00 ≤ P0≤ 0.00	
Unknown	55.70	0.0120	21	24.12	0.010	0.012	0.005 ≤ P0≤ 0.016	
Total	**4647.0**	**1**	**2012**	**2012**	**1**	**1**		

***** **Significant at $p \leq 0.05$**

+ **Selection for Tick Abundance Class**

- **Avoidance of Tick Abundance Class**

Table XII: Proportional availability and locations logged for eland across areas classified according to total tick abundance during February 2015. The data consists of the collective locations for four collared eland cows. Bonferroni confidence intervals (determined at the 95% level) were used to determine eland selection and avoidance according to tick abundance.

Total Tick Abundance	Total hectares	Proportion of total hectarage	Observed Number of Eland GPS Locations	Expected Number of Eland GPS Locations	Proportion Observed Locations per Abundance Class	Expected Proportion per Abundance Class	Confidence Interval on Proportion of Locations	
High	1146.29	0.2467	1497	843.86	0.438	0.247	0.416 ≤ P0≤ 0.460*	+
Moderately High	209.40	0.0451	0	154.15	0.000	0.045	0.000 ≤ P0≤ 0.000*	-
Moderate	140.05	0.0301	0	103.10	0.000	0.030	0.000 ≤ P0≤ 0.000*	-
Moderately Low	181.80	0.0391	0	133.83	0.000	0.039	0.000 ≤ P0≤ 0.000*	-
Low	2161.95	0.4652	1143	1591.55	0.334	0.465	0.313 ≤ P0≤ 0.355*	-
Unknown	807.56	0.1738	781	594.50	0.228	0.174	0.210 ≤ P0≤ 0.247*	+
Total	**4647.1**	**1**	**3421**	**3421**	**1**	**1**		

***** **Significant at $p \leq 0.05$**

+ **Selection for Tick Abundance Class**

- **Avoidance of Tick Abundance Class**

Table XIII: Proportional availability and locations logged for eland across areas classified according to adult tick abundance during February 2015. The data consists of the collective locations for four collared eland cows. Bonferroni confidence intervals (determined at the 95% level) were used to determine eland selection and avoidance according to tick abundance.

Adult Tick Abundance	Total hectares	Proportion of total hectarage	Observed Number of Eland GPS Locations	Expected Number of Eland GPS Locations	Proportion Observed Locations per Abundance Class	Expected Proportion per Abundance Class	Confidence Interval on Proportion of Locations	
High	681.84	0.1467	192	501.96	0.056	0.147	$0.046 \leq P0 \leq 0.066$*	-
Moderately High	1.36	0.0003	0	1.00	0.000	0.000	$0.000 \leq P0 \leq 0.000$	
Moderate	0.00	0.0000	0	0.00	0.000	0.000	$0.000 \leq P0 \leq 0.000$	
Moderately Low	994.20	0.2139	18	731.91	0.005	0.214	$0.002 \leq P0 \leq 0.008$*	-
Low	2913.87	0.6270	2710	2145.13	0.792	0.627	$0.774 \leq P0 \leq 0.810$*	+
Unknown	55.70	0.0120	501	41.01	0.146	0.012	$0.131 \leq P0 \leq 0.162$*	+
Total	4647.0	1	3421	3421	1	1		

***** **Significant at $p \leq 0.05$**

+ **Selection for Tick Abundance Class**

- **Avoidance of Tick Abundance Class**