

**VARIATION IN TICK COMMUNITY ACROSS DIFFERENT
CONTROL SYSTEMS, HABITATS, SEASONS AND
ENVIRONMENTAL FACTORS IN A MIXED CATTLE/WILDLIFE
RANCH: IMIRE GAME RESERVE, ZIMBABWE**

BY

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Abstract

An assessment of spatial and temporal variation in tick community diversity, abundance, sex ratio and age structure across habitats, seasons and tick sweeper types at Imire Ranch was carried out from March to September 2015. The study primarily aimed at establishing the efficacy of two chemically-treated tick sweepers (buffalo and cattle) in controlling free-living tick populations in a mixed cattle/wildlife ranch. A total of 5,124 ticks were recorded over the study period. *Rhipicephalus appendiculatus* was the dominant tick species, comprising 98.8% of adult ticks. *Rhipicephalus evertsi*, *Haemaphysalis leachi*, *Hyalomma truncatum* and *Hyalomma rufipes* comprised 0.92%, 0.16%, 0.05% and 0.11% of adult ticks, respectively. A single genus (*Rhipicephalus*) was recorded at nymphal stage and two (*Rhipicephalus* and *Amblyomma*) at larval stage, with *Rhipicephalus* being the most abundant. Tick abundance was at a peak during the hot-wet season and density greater in woodlands than in grasslands. There was a significant difference in the efficacy of the two sweepers with 4,274 ticks recorded in the buffalo-swept section and 850 in the cattle-swept section. Tick species richness was also higher in the buffalo-swept section (5) than in the cattle-swept area (3). *H. truncatum* and *H. rufipes* were only recorded in the buffalo-swept section. The efficiency of buffalo as a sweeper was lower in woodlands than in grasslands and much lower during the hot-wet season. In contrast, cattle were more efficient in woodlands and highly inefficient in the hot-dry season. Densities of all tick developmental stages (larvae, nymphs and adults) were significantly higher under buffalo sweeping, and were significantly different across seasons. Adult ticks were mostly abundant during the hot-wet season, while larvae and nymphs peaked during the cold-dry and hot-dry seasons, respectively. Tick larva and adults were more abundant in woodlands than grasslands, while nymphs were higher in grasslands. The tick community showed minor variation in sex ratio, with females being more abundant than males in *R. appendiculatus* and *H. truncatum*, while *R. evertsi* and *H. rufipes* were dominated by males. *Haemaphysalis leachi* had an equal number of males and females. Sex ratio was influenced by type of habitat, sweeper and season. There was weak correlation between tick density and grass sward height and non-linear relationship between tick abundance and soil moisture, temperature, grass height and mat depth. Canonical correspondence analysis showed an association of *Rhipicephalus* larva with sites with high sward height and high soil moisture, while *Rhipicephalus* nymph was associated with high humidity sites. Adult tick species were associated with sites with high mat depth, and they quested under low temperature. Among adult ticks, only *R. evertsi* and *R. appendiculatus*

preferred sites with high humidity. The study revealed that, even though acaricide-treated cattle are effective in controlling free-living ticks, the same cannot be said with buffalo. The difference is attributed to variations in stocking density and host susceptibility to infestation. An integrated tick control strategy that considers stocking rate, season and habitat type is recommended as an effective tick control strategy for cattle /wildlife mixed ranches.

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TABLE OF CONTENTS

ABSTRACT.....	i
ACKNOWLEDGEMENTS.....	iii
LIST OF TABLES.....	vi
LIST OF FIGURES.....	vii
CHAPTER 1	1
1 INTRODUCTION	1
1.1 Problem statement and justification	3
1.2 Aim of the study	4
1.3 Specific objectives of the study	4
1.4 Hypotheses.....	4
Chapter 2.....	6
2 LITERATURE REVIEW	6
2.1 Biology of ticks	6
2.2 Classification	7
2.3 Host finding strategies	8
2.4 Reproduction	10
2.4.1 Ixodidae (hard ticks).....	10
2.4.2 Argasidae (soft ticks)	12
2.5 Influence of environmental factors (abiotic factors)	12
2.6 Livestock/ wildlife interface	14
2.7 Tick-borne diseases	15
2.8 Tick control methods.....	17
2.8.1 Chemical control	17
2.8.2 Vaccination.....	24
2.8.3 Host resistance.....	25
2.8.4 Pasture spelling	26
2.8.5 Habitat modification.....	26
2.9 Tick control measures in Zimbabwe	27
CHAPTER 3	28
3 MATERIALS AND METHODS.....	28
3.1 Study area	28
3.1.1 Main section	29

3.1.2	Lodge section	30
3.2	The tick management strategy at Imire Ranch	31
3.3	Tick sampling	31
3.3.1	Drag sampling	32
3.3.2	Visual search method	33
3.3.3	Environmental variables/weather elements.....	33
3.4	Tick identification.....	34
3.5	Data analysis.....	34
CHAPTER 4	36
4	RESULTS	36
4.1	Tick abundance and species diversity at Imire Ranch.....	36
4.2	Efficacy of the two tick sweepers.....	37
4.2.1	Effect of season and tick sweeper	37
4.2.2	Tick sweeper and habitat.....	39
4.3	Species habitat preference	40
4.4	Developmental stage.....	41
4.5	Gender	44
4.5.1	Sex ratio of tick species.....	47
4.6	Environmental variables	48
chapter 5	52
5	DISCUSSION	52
5.1	Tick abundance and species diversity at Imire Ranch.....	52
5.2	Efficacy of the tick control regime at Imire Ranch	53
5.3	Spatial variation in tick abundance at Imire Ranch	55
5.4	Temporal variation in tick abundance at Imire Ranch	57
5.5	Influence of habitat and environmental factors on tick abundance at Imire Ranch	58
5.6	Sex ratio of ticks at Imire Ranch	60
5.7	Conclusion.....	61
REFERENCES	62

LIST OF TABLES

Table 2.1: Summary of categories of tick-borne diseases of humans and domestic or companion animals, with some representative examples (Sonenshine and Roe, 2014).....	16
Table 4.1: Ticks recorded in the two sections at Imire Ranch. [N = Number of ticks recorded, D = Density (ticks/29 m ²) and C = Composition of ticks (%)].....	36
Table 4.2: Total number of ticks (adults and immatures combined) in each habitat and section	40
Table 4.3: Discriminate classification matrix of habitats	41
Table 4.4: <i>R. appendiculatus</i> 's sex ratio and abundance of male and female ticks in the cattle and buffalo swept areas at Imire Ranch	47
Table 4.5: <i>R. appendiculatus</i> 's sex ratio and abundance of male and female ticks in the hot-wet and cold-dry season at Imire Ranch	48
Table 4.6: <i>R. appendiculatus</i> 's sex ratio and abundance of male and female ticks in grasslands and woodlands at Imire Ranch	48
Table 4.7: Tick density with variation in environmental variables at Imire Ranch.....	49
Table 4.8: Correlation coefficient values of environmental variables with tick density	50

LIST OF FIGURES

Figure 2.1: Physical features of hard ticks (Source: Walker <i>et al.</i> , 2003).	8
Figure 2.2: Physical features of soft ticks (Source: Walker <i>et al.</i> , 2003)	9
Figure 3.1: Map of Imire Ranch showing the two sections and study sites (yellow:grassland, red:woodland).	29
Figure 3.2: Sampling design of each transect used to sample ticks at Imire Ranch (ST: Sub transect, Q: quadrat).....	32
Figure 4.1: Mean abundance of different tick developmental stages across seasons	38
Figure 4.2: Seasonal mean tick densities in cattle and buffalo swept sections.....	38
Figure 4.3: Total number of ticks in woodlands and grasslands in relation to sweeper type ..	39
Figure 4.4: Cluster analyses of adult tick species and immature tick genus found at Imire Ranch	42
Figure 4.5: Total number of ticks in each developmental stage. Different lowercase letters indicate differences which are statistically significant ($P < 0.05$)	42
Figure 4.6: Total number of ticks in each developmental stage according to sweeper type ...	43
Figure 4.7: Total number of ticks in each developmental stage according to habitat	44
Figure 4.8: Total tick abundance of male and female ticks at Imire Ranch	44
Figure 4.9: Total number of ticks in each gender across sweeper types.....	45
Figure 4.10: Total number of ticks in each gender across seasons	46
Figure 4.11: Total number of ticks in each gender across habitats.....	46
Figure 4.12: Canonical correspondence output of interaction between tick species and environmental factors (humidity, temperature, soil moisture, sward height and mat depth) ..	51

CHAPTER 1

1 INTRODUCTION

Ticks are external parasites of mammals, birds and reptiles, that feed on blood (Jongejan and Uilenberg, 1994; Walker *et al.*, 2003). They damage animal skin, thus opening lesions for opportunistic secondary infections. Ticks are important vectors of animal and human pathogens. Diseases associated with them pose greater challenges to livestock health and management than tsetse-borne trypanosomiasis (Nyahangare *et al.*, 2012). In humans, they are the second most dangerous parasite after mosquitoes (Estrada-Peña, 2001). If infestations are heavy, they may cause toxicosis and paralysis to the animal. The most common tick-borne diseases in Africa are babesiosis, theileriasis (East Coast fever), cowdriosis and anaplasmosis (Nyahangare *et al.*, 2012). Tick impacts are greatest in developing countries. In Southern Africa, East Coast fever (ECF) alone killed around one million cattle in 1989 (Mukhebi *et al.*, 1992). Tick infestation is considered one of the major challenges to successful game ranching in Southern Africa (Horak, 1982).

Prolonged, intensive acaricide treatment, coupled with absence of significant numbers of wildlife hosts can reduce tick numbers in upland habitats (Norval *et al.*, 1994). However, if acaricide treatment of cattle is carried out in the presence of alternative hosts, eradication of *Amblyomma hebraeum* and *A. variegatum*, becomes difficult. This is due to the long attachment and feeding periods of the adult tick species and also attraction of unfed nymphal and adult ticks to infested hosts by a pheromone emitted by attached males (Norval *et al.*, 1994).

Tick species range is better explained by climate than host preference or vegetation-related variables (Cumming, 2002). Humidity controls the amount of time a tick can spend questing

before it gets dehydrated (Greenfield, 2011). A thicker mat depth preserves soil moisture and provides more niches for ticks. Some ticks are highly selective and may feed on one host species, while others may parasitize several host species (Oliver, 1989). Insufficient number of hosts or absence of key host species may limit tick species occurrence, although weather and other abiotic features may be permissive (Estrada-Peña *et al.*, 2013). Birds are an important carrier of ticks. They distribute them within and between continents, thereby extending their geographical range (Hubálek, 2004).

Suppression of grassland fires leads to a build up of tall grasses. This maintains or increases the tick reservoir (Fyumagwa *et al.*, 2007). Presence and abundance of ticks is related to vegetation type and density, since they both affect the local microclimate, thus influencing tick life cycles (Estrada-Peña *et al.*, 2013). Short grasses reduce tick survival due to reduced shed. Such habitats also favour such hosts as wildebeest, gazelle and hartebeest which have a relatively high innate resistance to ticks (Horak *et al.*, 1983). Thus, habitat variation and host community composition are likely to be key determinants of tick species composition, abundance and diversity.

The wildlife industry is becoming increasingly important in the economy of African countries, with greater economic and environmental benefits if integrated with livestock production (Chardonnet *et al.*, 2002; Western, 2013). Contact between livestock and wildlife in Southern Africa, however, can result in great livestock losses due to outbreaks of diseases such as foot and mouth (FMD), bovine tuberculosis, rinderpest and anthrax (Bengis *et al.*, 2002; Kock, 2005). The African buffalo, which is a long-term maintenance host of FMD, transmit it to cattle directly or through other species (Condy *et al.*, 1985; Bastos *et al.*, 2000). The only effective measure for the control of FMD is to separate infected buffalo herds from cattle (Kock, 2005).

1.1 Problem statement and justification

Globally, ticks and tick-borne diseases result in losses amounting to billions of dollars annually due to livestock mortality and expenses associated with tick control in the livestock industry (Jongejan and Uilenberg, 1994). The first step in controlling tick-borne diseases is the understanding of tick behaviour in relation to biotic and abiotic factors.

Imire Ranch is a mixed cattle/wildlife ranch that harbours different vegetation communities which are likely to define different animal habitats, communities and tick host species. There is always a high risk of tick-borne disease prevalence where livestock and wildlife closely interact. Cattle and buffalo at Imire Ranch are kept separately and graze across different vegetation communities. These animals act as tick sweepers. It is, however, not known whether this pattern of tick management creates tick community heterogeneity across different habitats.

Intensive chemical use, particularly acaricides, is primarily used to control tick and tick borne diseases (Jongejan and Uilenberg, 1994). Chemical tick control in wildlife areas is applied by spraying pastures or wildlife using self applicators (Duncan applicator). It is, however, more effective to allow livestock to collect ticks and then kill them on the host than applying acaricides to pastures (Jongejan and Uilenberg, 1994). The use of chemical tick control on livestock to control free living and parasitic tick populations in wildlife areas has been studied and proven feasible (Zieger *et al.*, 1998). Thus, use of cattle as tick sweepers is an alternative tick control method in cattle/wildlife areas. The integration of wildlife and livestock, however, results in increased tick-borne diseases, especially in areas with buffaloes (Bengis *et al.*, 2002). Buffaloes act as reservoirs of foot and mouth disease and *Theileria parva*, resulting in high cattle mortality when the two are integrated. So far, the only effective way of controlling the epidemic is through total separation of buffalo from cattle. This

control strategy is, however, not practical in areas where buffalo co-habitat with cattle. The present study sought to establish whether intensive chemical tick control applied to a wildlife species (buffalo) can produce an equally effective means of tick control as that applied to livestock (cattle). If this is the case, this therefore could provide an alternative approach to tick-borne diseases control and management of free-living and parasitic tick populations in wildlife areas.

1.2 Aim of the study

The study sought to establish spatial and temporal variations in tick community, diversity, abundance, sex ratio and age structure across habitats, seasons and tick sweeper types at Imire Ranch.

1.3 Specific objectives of the study

The specific objectives of the study were:

- to establish whether the efficacy of the two tick sweepers used at Imire Ranch are significantly different across habitats and seasons;
- to establish whether tick life stage differs with season, tick sweeper and habitat;
- to establish whether tick gender differs with season, tick sweeper and habitat; and
- to determine the influence of weather and environmental factors on tick composition and density.

1.4 Hypotheses

- H_0 : There is no significant difference between the two tick control regimes across habitat and season.

- H_0 : Season, habitat and tick sweeper do not influence tick's developmental age.
- H_0 : Season, habitat and tick sweeper does not influence tick gender.
- H_0 : Weather and environmental factors do not influence tick composition and density.

CHAPTER 2

2 LITERATURE REVIEW

2.1 Biology of ticks

Ticks are invertebrates that belong to phylum Arthropoda, order Acari, which includes mites (Walker *et al.*, 2003). They primarily belong to two families, Argasidae (soft ticks) and Ixodidae (hard ticks). A third family, Nuttalliellidae, is monotypic, with no medical importance (Service, 2008). Hard ticks have hard dorsal shields, while soft ticks have a flexible leathery cuticle (Jongejan and Uilenberg, 1994). Ticks are blood-feeding parasites that lack wings and antennae (Walker *et al.*, 2003). They comprise of at least 840 species. Approximately 80% of all tick species, including those of greatest economic importance, belong to the family Ixodidae (Jongejan and Uilenberg, 1994). Although a small proportion of tick species belong to the family Argasidae, they also play a significant role as vectors of diseases, especially in poultry.

The tick body is made up of three regions, namely, the capitulum, idiosoma (the body) and legs (Sonenshine and Roe, 2014). The capitulum is attached to the anterior of the body by the basis capituli. It includes leg-like palps, hypostome (with rows of recurved teeth for attachment) and chelicerae (for cutting, ripping and tearing skin). When attaching to a host, the hypostome penetrates the skin and the chelicerae cut a hole in the dermis and break the capillary vessels close to the skin, thus forming a feeding lesion (Walker *et al.*, 2003). The palps are glued to the outer epidermis by material secreted in the tick's saliva.

The idiosoma is subdivided into an anterior region (podosoma) where four pairs of legs are attached and a posterior region (opisthosoma) that bears the spiracular plate and anal aperture (Sonenshine and Roe, 2014). These subdivisions have, however, been masked by extreme

fusion. The legs are divided into six segments and articulate with the body by the coxae. They have a sensory organ (Haller's organ) situated on the front tarsi that is used to detect odour and environmental factors such as humidity, temperature and carbon dioxide levels (Greenfield, 2011; Sonenshine and Roe, 2014).

Different age classes take different times to fully engorge with blood (larvae 3-5 days, nymphs 4-8 days and females 5-20 days). Males mostly feed to enable their reproductive organs to mature, and do not expand like females (Walker *et al.*, 2003).

2.2 Classification

Tick larvae have three pairs of legs and no genital aperture, while nymphs have four legs and no genital aperture (Walker *et al.*, 2003; Greenfield, 2011). Adults have four pairs of legs and a genital aperture which is larger in females. All female ixodid ticks have a scutum which partially covers the idiosoma, enabling the tick to engorge with blood, while males have a conscutum which covers the whole idiosoma as shown in Figure 2.1 (Greenfield, 2011). Argasid ticks lack the scutum, but have a leathery, folded cuticle (Sonenshine and Roe, 2014). The cuticle unfolds during feeding, enabling them to rapidly consume blood (within minutes to 2 hours). Adults and nymphs of soft ticks have their mouthparts situated ventrally as shown in Figure 2.2 (Service, 2008). The capitulum therefore is not visible dorsally, in contrast to that of hard ticks which projects outwards and is visible dorsally as illustrated in Figure 2.1. Larvae of both soft and hard ticks, however, have their capitulum visible dorsally. Larvae and nymphs are usually assigned in the correct genus by comparing their mouthparts, coxae and other features as done on adult ticks (Walker *et al.*, 2003). Some of the physical features of hard and soft ticks are illustrated in Figure 2.1 and Figure 2.2, respectively.

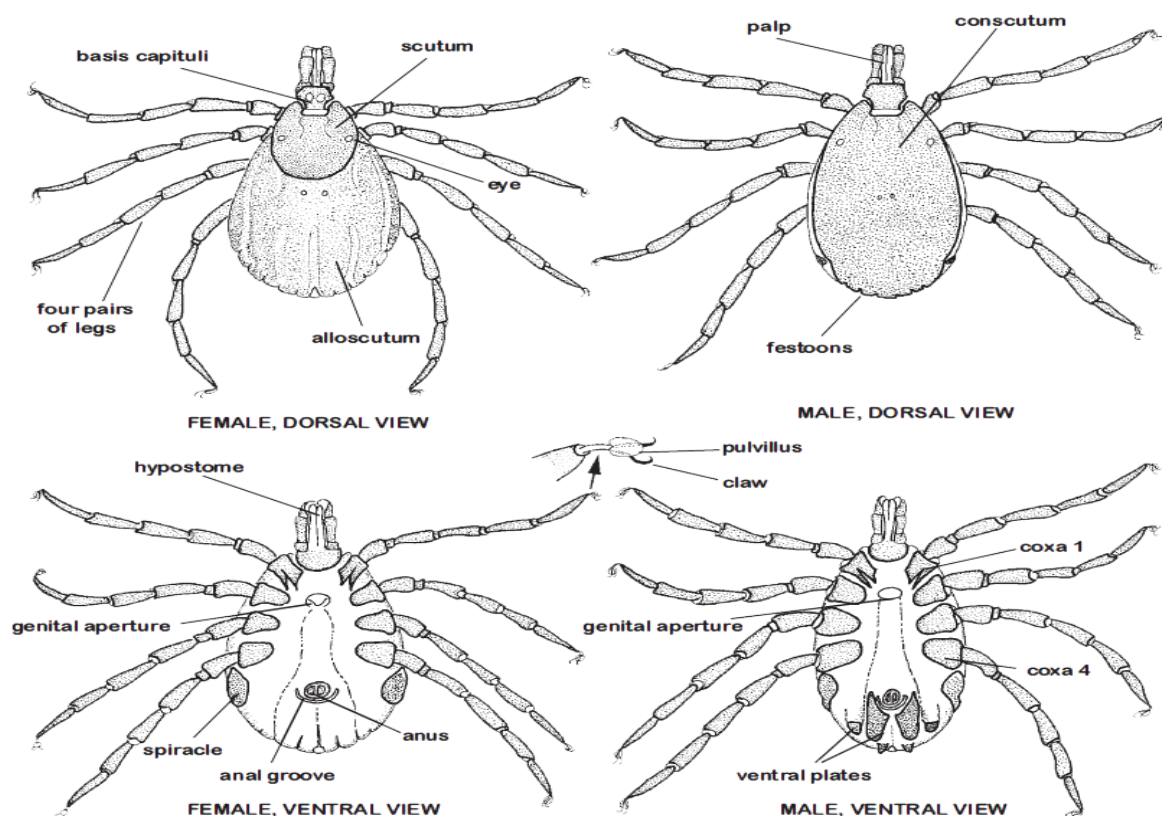


Figure 2.1: Physical features of hard ticks (Source: Walker *et al.*, 2003).

2.3 Host finding strategies

Ticks use several ways to locate hosts. Some quest, i.e. they crawl onto vegetation and wait for passing hosts which they grab onto using their front legs, then crawl on the host until they find a suitable site to attach and feed (Walker *et al.*, 2003). The tick's questing behaviour is related to host kairomones which are residues rubbed off host body onto vegetation (Terassini *et al.*, 2010). Ticks become akinetic upon encountering residues of kairomones (Carroll, 1998). As Artiodactyla and Peryssodactyla usually frequent the same trails (Emmons and Feer, 1997), ticks waiting on these positions have a chance of successfully encountering the host (Carroll, 2003). Arrestment pheromones present in cast larval skins, tick faecal droppings and tick body exudates also induce akinetic (Sonenshine and Roe, 2014). These

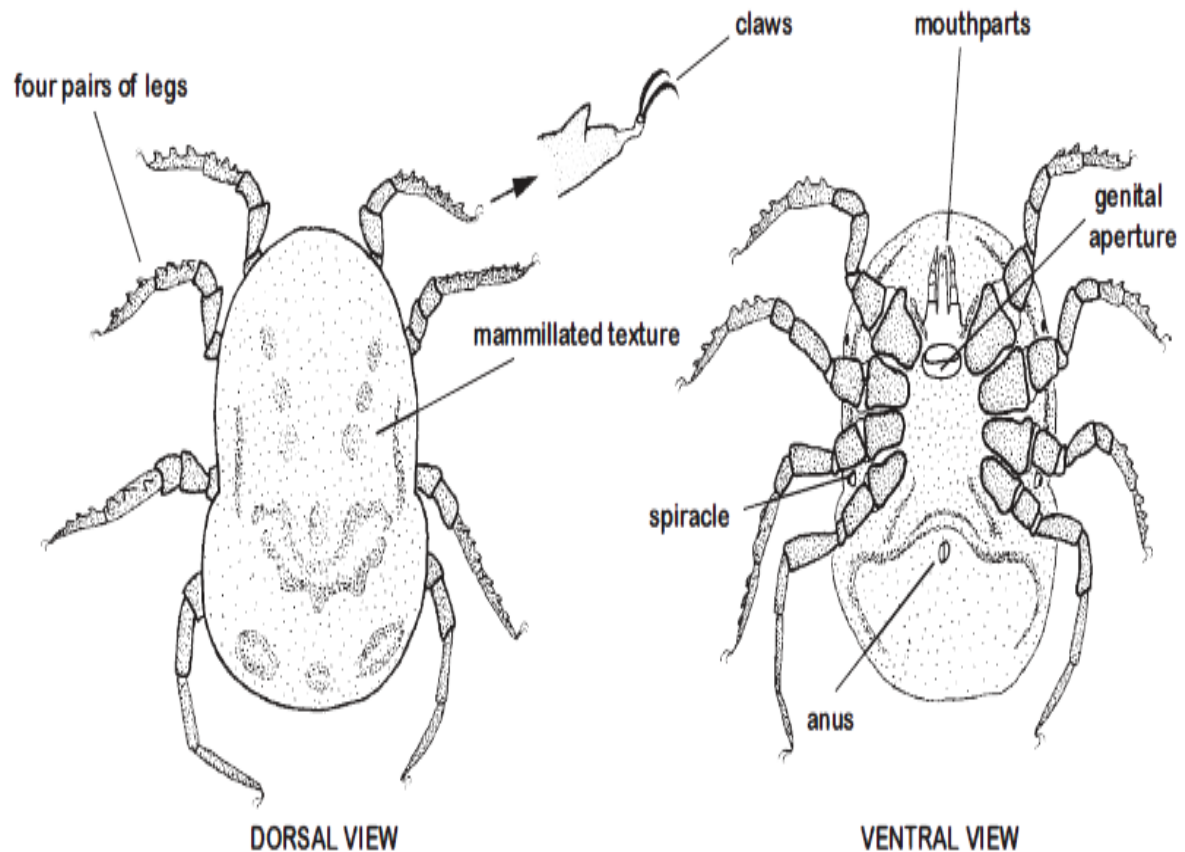


Figure 2.2: Physical features of soft ticks (Source: Walker *et al.*, 2003)

two pheromones result in clustering of ticks. The arrestment pheromones are interspecies specific, i.e. *Ornithodoros moubata* arrestment pheromones induce cessation of movement in *O. tholozani* (Sonenshine, 2004). This behaviour is also expressed between some different genera (Sonenshine and Roe, 2014).

Adult *Amblyomma* and *Hyalomma* are exophilic, i.e. they hunt for a nearby host by running across the ground (Walker *et al.*, 2003). Argasids and many *Ixodes* species are endophilic, i.e. they spent their life time in a host's nest from where they attach to available host. A few species of ticks have adapted to human dwellings, e.g. *Rhipicephalus sanguineus*. These feed on domestic animals living there. This is called domestic behaviour (Walker *et al.*, 2003).

A particular tick species may be absent when there are insufficient numbers or absence of key hosts also known as tick maintenance hosts, even when weather conditions and other abiotic factors are favourable (Estrada-Peña *et al.*, 2013). Ticks, however, can survive long periods without feeding with adults able to live for one to two years and occasionally seven years as long as they are under suitable conditions (Ashford, 2001).

2.4 Reproduction

2.4.1 Ixodidae (hard ticks)

Different tick species have different host life cycles (Walker *et al.*, 2003). Hard ticks exhibit four life stages in their life cycle, namely egg, larva, nymph and adult (Jongejan and Uilenberg, 1994; Sonenshine and Roe, 2014). They take a blood meal only once at each instar and spent long periods on vegetation searching for hosts. Male ticks mate with many feeding females on the host (Walker *et al.*, 2003). *Ixodes* may also mate when they are still on vegetation. They remain attached for a long time and mate with many females before they die (Jongejan and Uilenberg, 1994). They transfer a sac of sperms (spermatheca) to the females which mate only once before they fully engorge with blood. Enough sperms to fertilise all eggs are transferred at this single encounter. The female detaches from the host after it is fully engorged with blood and scouts for a sheltered place for oviposition (Jongejan and Uilenberg, 1994). She lays a single, large batch of between 2,000 and 20,000 eggs on the physical environment, before it dies (single gonotrophic cycle) (Jongejan and Uilenberg, 1994; Walker *et al.*, 2003; Sonenshine and Roe, 2014).

2.4.1.1 Three host tick life cycle

Most hard ticks require three different hosts to complete their life cycle (Jongejan and Uilenberg, 1994). The larva develops in the egg and hatches (Walker *et al.*, 2003). The

hatched larva seeks for a host and feeds once. It detaches and hides in the soil/vegetation where it moults to a nymph. The nymph seeks for a host and feeds once before it detaches and moults to an adult tick (female or male), which seeks and climb onto a new host. An adult female feeds and mates once, then detaches itself from the host to the ground where it lays eggs before it dies. An adult male may feed and mate several times before it dies. The life cycle may take six months to several years, as the parasitic phase of each species varies (Randolph, 2004). Ticks spend the majority of their life cycle searching for a host, and three host ticks have to scout three successful times to complete their life cycle thereby also contributing to the great variation in the time period taken to finish a tick's life cycle (Randolph, 2004). Questing and moulting is hindered by morphological and behavioural diapause in the harsh winter season. All these factors result in great variation in the duration of tick life cycles.

2.4.1.2 Two host tick life cycle

The hatched larva mounds a host, feeds and moults to a nymph whilst still attached to the same host (Walker *et al.*, 2003). The fed nymph detaches to the ground where it moults to an adult. The adult tick finds a new host on which it feeds and mates. It later detaches to lay eggs (female) or dies (male). Common examples are *Rhipicephalus evertsi evertsi* and *Hyalomma detritum detritum* (Walker *et al.*, 2003).

2.4.1.3 One host tick life cycle

The hatched larva attaches to a host and feeds (Walker *et al.*, 2003). It does not detach, but moults to a nymph while attached to that host. The nymph feeds and moults to an adult whilst still attached to that same host. The adult tick also feeds and mates on that same host, although positions of attachment may change in order to find a mate. Thus, all three life

stages are completed on one host. Examples of one host species are all *Boophilus* sub genera of genus *Rhipicephalus* (Walker *et al.*, 2003).

2.4.2 Argasidae (soft ticks)

Most argasid ticks are multi-host ticks (Walker *et al.*, 2003). The larvae of some species feed rapidly (few minutes to hours) or over several days before they detach and moult (Jongejan and Uilenberg, 1994). In some argasids, however, the larvae do not feed, but moult directly to the first nymphal stage (Walker *et al.*, 2003). The first nymphal stage feeds rapidly and moults to a further nymphal stage before detaching. Similar feeding progresses for a variable number of nymphal stages, but on different individual hosts. When the nymph moults to an adult, the adult female feeds rapidly on a host, detaches and lays a small batch of eggs (100-500). Mating does not occur on the host. The females repeat feeding and laying eggs for up to six times before they die (multiple gonotrophic cycle) (Walker *et al.*, 2003; Sonenshine and Roe, 2014). Argasid ticks remove excess water through the coxal apparatus located in the proximal part of the front pair of legs (Jongejan and Uilenberg, 1994). This concentrates their blood meal. They are able to survive starvation and resist long periods of hot and dry conditions without a blood meal due to their several nymphal instars and several adult blood meals (Jongejan and Uilenberg, 1994). Several instars also allow them to have a long life span of up to 20 years compared to ixodids which only last for one, two or three years (Sonenshine and Roe, 2014).

2.5 Influence of environmental factors (abiotic factors)

Ticks spend the majority of their life cycle free-living on the environment under the influence of such abiotic factors such as climate and habitat structure (Randolph, 2004). Vegetation influences the micro-climate of an area (Randolph and Storey, 1999). The presence and abundance of ticks is related to vegetation type and cover as they modify the local

microclimate at the level that ticks quest, thus affecting the tick life cycle (Tälleklint-Eisen and Lane, 2000; Estrada-Peña *et al.*, 2013). Short grasses reduce tick survival due to reduced shade (Horak *et al.*, 1983). This results in tick death due to desiccation and ultraviolet radiation. Such habitats also favour such hosts as wildebeest, gazelle and hartebeest which have relatively high innate resistance to ticks. Vegetation density also influences host abundance, thereby affecting tick attachment successes (Estrada-Peña *et al.*, 2013). However, during tick sampling, vegetation cover affects the efficiency of dragging and flagging, thereby distorting the abundance of ticks obtained per drag (Tälleklint-Eisen and Lane, 2000).

Temperature is one of the main factors that influence tick phenology (Estrada-Peña *et al.*, 2013). Most ixodid ticks are inactive in the lower part of vegetation or leaf litter, and are triggered by a set of suitable conditions such as temperature. Ticks climb up vegetation to quest under suitable temperature. However, only the temperature between the questing height and the ground can be related to tick activity as it affects ticks rather than atmospheric temperature measured at a height of 2 m (Estrada-Peña *et al.*, 2013). Low temperatures affect tick activity, reducing questing until temperature becomes permissive (Randolph, 2004).

When ticks quest, they actively lose moisture and regain it by descending at intervals to the lower parts of the litter zone where they re-absorb moisture from the atmosphere (Kahl and Alidousti, 1997). Different tick species have different abilities of retaining or absorbing moisture (Estrada-Peña *et al.*, 2013). This results in some species becoming endemic in certain areas, such as the camel tick that is adapted to xeric habitats (Randolph, 2004). Water loss in ticks is influenced by saturation deficit, while absorption is influenced by relative humidity and intrinsically affected by the ability of the tick to locate a place with a suitable micro-climate, even when the weather is hot and dry. Low saturation deficit results in longer tick questing before they retire to vegetation litter where they absorb moisture, which in turn

increases their chances of successfully finding a host. However, there is a critical equilibrium humidity below which ticks fail to re-absorb from the atmosphere (Estrada-Peña *et al.*, 2013). Tick survival, therefore, diminishes in low humidity even if the saturation deficit is low, as they fail to actively absorb moisture. In areas of high humidity, moisture deficit has less effect as ticks can actively absorb moisture, replenishing the lost moisture. A mat (vegetation litter) plays a role in preserving soil moisture when it is thick, and removal of litter increases tick desiccation (Greenfield, 2011). It also provides more niches for ticks to occupy.

Ticks have a photoreceptor and a clock which measures day and night lengths (Berkvens *et al.*, 1994). This regulates growth and development. Photoperiod (day-night relative change) influences the behavioural diapause of unfed ticks, while it affects morphological diapause in engorged ticks (Randolph, 2004; Estrada-Peña *et al.*, 2013). It enables the tick to find a host, feed and moult before onset of such harsh environmental conditions as winter. However, reduced day length beyond a critical level induces diapause rather than absolute day length. Behavioural diapause is the suppression of host-seeking activity in unfed ticks. Adult ticks that moult at the onset of harsh conditions (revealed by photoperiod) delay questing until desirable conditions prevail. Morphological diapause is the blocking of such essential developmental stages as metamorphosis and embryogenesis (Berkvens *et al.*, 1994).

2.6 Livestock/ wildlife interface

Due to Africa's extensive and diverse wildlife resources, the wildlife industry is becoming increasingly important in the economies of its countries (Chardonnet *et al.*, 2002). It offers a competitive advantage over the rest of the world, attracting lucrative tourists (Kock, 2005). The revenue generated can be channelled towards the local community thereby alleviating poverty especially in times of drought when agriculture and livestock production are not fruitful. Coupling wildlife with livestock production realises greater economic and

environmental benefits (Western, 2013). Contact between livestock and wildlife may result in great livestock losses due to an increase in tick-borne disease incidence (Bengis *et al.*, 2002). The diseases of most concern are bovine tuberculosis, rinderpest, anthrax and foot and mouth (FMD). Ungulates, mainly in the family Bovidae, are the main species reported in wildlife/livestock disease outbreaks. The diseases can be mitigated by strict land-use policies, animal movement controls and fencing (Thomson, 1995).

2.7 Tick-borne diseases

Tick and tick-borne diseases are an important cause of loss in the livestock industry, amounting to billions of dollars annually due to livestock mortality and tick control operations (Jongejan and Uilenberg, 1994). Their effects are pronounced due to their ability to transmit a wide range of pathogenic micro-organisms such as protozoa, bacteria and viruses (Table 2.1). The most important diseases of domestic ruminants in tropical and sub-tropical areas are theileriosis and babesiosis (protozoan) and anaplasmosis and heartwater (rickettsial diseases) (Uilenberg, 2012). Ticks of the genus *Ixodes* and the species *Ornithodoros lahorens* are associated with a toxin which causes paralysis of the host (Muhammad *et al.*, 2008). Soft ticks are known to transmit tick-borne relapsing fever in humans (Service, 2008).

Effects of tick infestation include stunted growth and weak and thin young animal hosts. In dairy cows, this may result in reduced milk production (Muhammad *et al.*, 2008). Infestation may also result in significant depreciation in the value of skin and hides (Biswas, 2003). Adults of *Amblyomma variegatum* are known to cause scarring of cattle teats, thereby reducing suckling efficiency (Walker *et al.*, 2003). They also reduce host immunity, rendering it susceptible to such skin diseases as dermatophilosis. Ixodid ticks consume a lot of blood which results in significant blood loss of hosts (Sonenshine and Roe, 2014). Huge

tick loads may result in death due to exsanguinations. They may also render the host susceptible to other diseases (Sonenshine and Roe, 2014).

Table 2.1: Summary of categories of tick-borne diseases of humans and domestic or companion animals, with some representative examples (Sonenshine and Roe, 2014)

Category of causative agent	Representative disease	Causative agent	Major tick vector(s)	Primary affected host(s)
Protozoa	Babesiosis	<i>Babesia bigemina</i> , <i>B. microti</i> , etc.	<i>Rhipicephalus</i> spp.	Cattle, deer
	East coast fever	<i>Theileria parva</i>	<i>Rhipicephalus appendiculatus</i>	Cattle, African/cape buffalo
	Theileriosis	<i>T. annulata</i>	<i>Hyalomma</i> spp.	Cattle, water buffalo
	Human babesiosis	<i>B. microti</i>	<i>Ixodes scapularis</i> , <i>I. ricinus</i>	Humans, mice
Bacteria	Rocky Mountain spotted fever	<i>Rickettsia rickettsii</i>	<i>Dermacentor</i> spp.	Humans, dogs, small mammals
	Mediterranean spotted fever	<i>R. conorii</i>	<i>Rhipicephalus sanguineus</i>	Humans, hedgehogs, small mammals
	Anaplasmosis	<i>Anaplasma phagocytophilum</i>	<i>I. scapularis</i> , <i>I. ricinus</i> , others	Humans, deer, dogs, others
	Human ehrlichiosis	<i>Ehrlichia chaffeensis</i>	<i>Amblyomma americanum</i>	Humans, deer
	Canine ehrlichiosis	<i>E. canis</i> , <i>E. ewingii</i>	<i>R. sanguineus</i> , others	Dogs
	Heartwater	<i>E. ruminantium</i>	<i>A. hebraeum</i> , <i>A. variegatum</i>	Cattle, other ruminants
	Q fever	<i>Coxiella burnetii</i>	Various spp	Cattle, humans, other mammals
	Lyme disease/lyme borreliosis	<i>Borrelia burgdorferi</i> , other <i>Borrelia</i> spp.	<i>I. scapularis</i> , <i>I. ricinus</i> , others	Humans, diverse mammals, birds
	Tick-borne relapsing fever	<i>Borrelia</i> spp.	Various <i>Argasid</i> spp.	Humans, other mammals
	Tularemia	<i>Francisella tularensis</i>	<i>Haemaphysalis leporis-palustris</i> , <i>Dermacentor</i> spp., others	Lagomorphs, humans, other mammals
Virus	Tick-borne encephalitis	<i>Flavivirus</i>	<i>I. ricinus</i> , other <i>Ixodes</i> spp.	Rodents, humans, other mammals
	Colorado tick fever	<i>Coltivirus</i>	<i>D. andersoni</i>	Humans, various mammals

Fungus (<i>Actinomy</i> <i>cetales</i>)	Crimean-congo hemorrhagic fever	<i>Nairovirus</i>	<i>Hyalomma</i> spp.	Humans, lagomorphs, hedgehogs, etc.
	African swine fever	<i>Iridovirus</i>	<i>Ornithodoros porcinus</i>	Pigs, warthogs
	Dermatophilosis	<i>Dermatophilus congolensis</i>	Tick-associated, no proven transmission	Cattle, other domestic animals
Tick	Tick paralysis	Tick-transmitted proteins	Many tick spp.	Humans, cattle, other domestic animals, birds, etc.
	Tick toxicosis, tick-bite allergies	Tick-transmitted proteins	Many tick spp.	Humans, cattle, sheep, other mammals, birds

2.8 Tick control methods

2.8.1 Chemical control

Application of acaricides is the most commonly used method, for tick control. It however, leads to selection of tick species resistant to acaricide treatments, e.g. *Rhipicephalus (Boophilus) decoloratus*, *R. evertsi*, *R. appendiculatus* and *Rhipicephalus (Boophilus) microplus*, while other species die (Gono *et al.*, 2014). The chemicals are also toxic, often leaving residue in meat and milk. In addition, they are expensive, both in their acquiring and application (Mapholi *et al.*, 2014). In areas of extremely high tick populations coupled with acaricide resistance, chemical control is no longer sustainable. Efficient tick control through dipping, results in reduced immunity among animals such that any disruption of the dipping regime is likely to result in high mortality due to tick-borne diseases (Jongejan and Uilenberg, 1994). There are various strategies for the application of acaricides depending on the tick species and livestock production systems as explained in sections that follow (Jonsson, 2004).

Absolute tick control

The method involves complete tick control against introduced ticks, in areas which are free from ticks, but adjoining tick-infested areas or areas where complete tick eradication was successful (Jonsson, 2004). These are quarantine areas, and movement of livestock between and within such areas is controlled. Monitoring, inspection of livestock and compulsory eradication of possible infestation are some of the measures implemented in this control.

Absolute tick control in marginal or controlled areas

This involves the use of legislation to support control measures that eradicate ticks from areas marginally suited for them (Jonsson, 2004). The control strategy takes into account the tick life cycle. Duration between the first acaricide treatment and end of the control period should be more than the free-living phase of the tick. This ascertains that all ticks find a host before acaricide treatment is stopped. In conjunction with this consideration, the interval between two successive treatments should be less than its parasitic phase, ensuring acaricide treatment of every attached tick before it detaches.

Strategic control

In strategic control, applications are done at times of the year when there is peak tick abundance (Jonsson, 2004). Application of the acaricide from the commencement date to the end of the control phase is, however, applied at the interval postulated without taking into consideration the number of ticks on the host at the time of dipping. The interval is maintained, although tick populations might have reduced or increased.

Opportunistic control

This strategy is employed in areas where it is expensive to assemble animal hosts (Jonsson, 2004). Animals are thus treated with an acaricide on occasions when they are assembled for

other purposes such as branding, tagging or castration. Tick control, therefore, is left to the opportunity of other crucial activities that necessitate the assembling of animals.

Prophylactic treatment

This involves the application of an acaricide until the tick population is low enough not to cause mortality due to infestation or tick-borne diseases (Jonsson, 2004). As maintaining intensive chemical tick control strategies are expensive, this strategy reduces operational costs and mortality. It is usually employed with pour-ons and injectible acaricide which have a long time effect.

Threshold treatment

Acaricide treatment is commenced once a certain maximum number of ticks are observed on the hosts (threshold) (Jonsson, 2004). A representative number of hosts are surveyed for ticks, and the tick population per animal determined. The threshold approach, however, also takes into account the reproductive capacity of the ticks. It thus varies with time of year. It is lower in early summer than in late summer as reproduction is higher at the onset of summer. For example, tick numbers of 30 per animal may result in commencement of acaricide treatment in early summer as they are likely to produce more offspring. However, the same number might not result in commencement of acaricide treatment in winter as reproduction is low. The economic threshold can be estimated by the formula below:

$$n = c \times \frac{10^3}{Pdk t}$$

Where n = the number of standard ticks per animal

c = the cost of dipping per beast (\$)

P = the price of beef per kg live weight (\$)

d = the damage coefficient or loss (g) in live weight per engorging tick,

k = the proportion of parasitic ticks killed by each dipping

t = the mean number of days that each tick is parasitic on the host (Sutherst *et al.*, 1983)

Selective control

In selective control, acaricide treatment is applied only to animals with a tick burden above the economic threshold (Jonsson, 2004). Acaricide treatment is selectively applied to only individual hosts with a huge tick burden that can affect production. The rest of the herd is not treated. These animals, however, show low host resistance to ticks and would be beneficial to remove these individuals as they may pass these traits to their offsprings. This strategy reduces treatment costs as acaricide application only targets heavily infested animals.

Integrated tick control

This involves the use of several complementary control strategies without relying on one method to achieve better use of each control strategy (Nari, 1995). It can incorporate elements of threshold, absolute, strategic and opportunistic control to enhance tick management (Jonsson, 2004). It also includes such other control methods as biological, vaccination and host resistance for successful control. The future of tick control lies in the integrated use of different control methods as using one method alone is not sufficiently robust (Willadsen, 1980).

2.8.1.1 Acaricide application

The interval between acaricide applications depends on the biology of the tick (Seifert, 1996) as it should not exceed the fastest feeding time of the tick. For example, *R. appendiculatus* is a rapid feeder, and each stage can engorge within 4-7 days. Thus, the dipping interval should

be 4-5 days. The interval can also be influenced by the characteristics of the acaricide as they differ in their residual effect.

There are various ways used to apply acaricides on the animals. These methods include spray race, plunge dip or dipping tank, hand dressing, hand-spraying, pour-on and self-applicator (the Duncan applicator).

Plunge dip/dipping tank

This method was designed for the application of arsenic to control ticks (Seifert, 1996). Arsenic only affects ticks upon reaching the trachea, thereby making it essential to completely immerse the whole animal in acaricide. Arsenic is cheap, hence the 20 m³ of water used is not costly. The use of costly, modern acaricides is, however, prohibitively expensive for small famers. In addition, the construction of a dip tank is very expensive (Seifert, 1996).

Careful consideration should be made when one sites a dip tank (Seifert, 1996). It should be at a site where disposing the utilised dip liquid does not cause environmental hazard, i.e. away from rivers, but close to a water source. It should be close to pastures to reduce travelling time of animals and on a hill or slope to allow rain water to drain away from the dip. The treated water can be used for several months, but there is need to carefully monitor the concentration of the dip liquid after each dip as some of the active ingredients are carried out of the dip by the animals during dipping, thereby reducing the dip liquid concentration (strip out effect). Evaporation also affects the concentration as well as dirt, especially from dung. Acaricide and water can be added to maintain the appropriate concentration, however, there is a risk of over concentration or below strength concentration (Seifert, 1996).

Spray race

A spray race is 4-5 m long, with walls on its side fitted with three nozzles to spray on both sides of the animal and on the perineum which is the favourite attachment site for ticks (Seifert, 1996). Compared to a dip, spray race utilises less water and acaricide, making it less expensive. Tick acaricide resistance due to below strength acaricide is reduced as the correct strength is freshly made at each spray. However, as the drip-off liquid is drained into a storage tank and reutilised on that spraying regime, the concentration is affected by the strip out effect. There is no risk of poisoning due to over concentration and drinking by animals. Furthermore, animal injuries are rare.

Hand spraying

A high pressure hand pump/ knapsack is used to spray each animal (Junquera, 2015). It is the most used method by small famers in developing countries. The animal should be immobile to adequately spray it completely. This method, however, is only ideal when a few animals (less than 20) are being treated as it is labour-intensive. There is no collection of dipping fluid that drains off the sprayed animals, thereby wasting the acaricide.

Pour-on and self-applicator

Pour-on involves the use of etheric oils which spread on the animal coat and affect ticks feeding far from the application site (Seifert, 1996). The acaricide is applied on the top line from the pole to the tail. Pour-ons only require a holding pen for application of the acaricide. Therefore, no huge installation costs required. For wildlife, this method is done using a self-applicator like the Duncan applicator. Animals are attracted to the machine by a lick. The pour on is applied to the ears, neck and face by rollers carefully positioned on the applicator. Grooming also facilitates spreading of the pour-on to the rest of the body.

Chemical tick control on livestock to control free-living and parasitic ticks

In wildlife areas, application of chemical tick control on livestock, regulates the population of free living ticks and parasitic ticks on wildlife when they are kept together (Horak and Knight, 1986; Zieger *et al.*, 1998). Livestock is flooded into wildlife areas, thereby becoming infested with ticks which are eradicated by intensive acaricide treatment at regular intervals. The livestock acts as sinks, sweeping ticks which are exterminated before they become fully engorged and drop for moulting or laying eggs. As one female tick lays between 2 000 and 20 000 eggs (Walker *et al.*, 2003), eradication of all female ticks on the livestock results in considerable reduction in tick populations in the area. In turn, intensive chemical tick control on the livestock would effectively regulate tick burdens on wildlife in turn diminishing the chances of them acting as tick sources for livestock (Horak and Knight, 1986).

2.8.1.2 Acaricide resistance

Tick control heavily relies on acaricide application, and tick resistance poses a threat to successful tick control (Felix *et al.*, 2013). Tick resistance is influenced by acaricide usage and tick life cycle. Multi-host tick species have longer life cycles as compared to single host species. They spend significant periods searching for a host, with a short period spent on actual feeding. The acaricide application interval for most farmers is usually greater than the parasitic periods. A higher proportion of ticks in any generation is, therefore, likely to escape acaricide treatment. Single host species with a short life cycle, therefore, produce large numbers of larvae many times each year, thereby necessitating the increase in acaricide application to affectively control outbreaks. Thus, tick resistance is less of a problem in multi-host species than in single host species (Mekonnen *et al.*, 2002). The application of products with acaricidal activity to control other parasites might interfere with tick acaricide resistance. For example, the use of synthetic pyrethroids to control *Glossina* species (tsetse flies) on livestock so as to prevent transmission of trypanosomes in Africa influences the

resistance of ticks in the vicinity (Felix *et al.*, 2013). The most effective way to test acaricide efficacy is to test it under field conditions as it reflects the conditions under which the tick, host and acaricide are subjected to. It takes into account the environmental variation and behavioural factors that affect it. This can be effected through treating a small number of animals first before applying the acaricide to a larger number of animals (Felix *et al.*, 2013).

With the high cost of pesticide research, development and registration, it is ideal to adopt acaricide practises that delay tick resistance (Felix *et al.*, 2013). This can be achieved by reducing the frequency of application, modification of dose or concentration, use of mixtures of different chemistries and different modes of action, use of synergists, rotation between acaricide classes having different targets of action, preservation of untreated refugia, application of bio-security protocols to prevent introduction of resistant ticks and development and use of monitoring tools to detect resistance before product failure. Piperonyl butoxide is used as a synergist for pyrethroid acaricides to control pyrethroid-resistant ticks (Felix *et al.*, 2013).

2.8.2 Vaccination

Vaccination can be carried out which results in an immune response in cattle against tick-borne diseases. This is applied through gut antigens rather than salivary antigens (Jongejan and Uilenberg, 1994). Two similar vaccines have been produced, namely Gavac[®] (Heber Biotec S.A., Havana, Cuba) and TickGARD[®] (Intervet Australia Pty. Ltd., 91-105 Harpin Street, Bendigo East, Victoria, Australia). They both use the same gene Bm86, a concealed gut antigen which results in damage to the tick gut upon feeding (Kemp *et al.*, 1989). Immunization can also be executed by injecting blood containing infective or attenuated organisms or using infected tick stabilates (Dolan, 1992).

2.8.3 Host resistance

Within a host species, there are certain breeds which are able to limit the number of ticks on their bodies, e.g. Zebu cattle (*Bos indicus*) in Australia (Jongejan and Uilenberg, 1994). Zebu cattle are more resistant to ticks than Taurine cattle (*Bos taurus*). This can be achieved by tick avoidance strategies, grooming, or characteristics of their skin, or resistance to tick infestation. Crosses between Zebu and Taurine cattle result in intermediate resistance. Host resistance within a certain breed/ species also differs, with certain individuals possessing a greater ability to limit tick load on their bodies over others. Host resistance reduces the number of ticks on a host (Willadsen, 1980). It also lowers the tick engorgement weight (blood meal amount) and egg production of engorged females. This in turn reduces the number of larvae produced in the next generation, thereby lowering the tick population in the area.

Tick resistance can be present from birth (innate natural resistance) or acquired in response to tick exposure (acquired natural resistance) due to the host's immunological reaction towards the exposed antigens of the parasite (Allen, 1989; Osofsky *et al.*, 2005). However, tick resistance is heritable and is largely determined by the animal's physiological condition. The animal's resistance may deteriorate due to stress, disease, lactation and malnutrition. It can also fluctuate with season, with low resistance in the winter due to malnutrition. However, for an animal to maintain a level of resistance, it should be in regular contact with ticks (Jongejan and Uilenberg, 1994). Thus, total eradication of ticks is not recommended as it lowers host immunity to tick-borne diseases. Introduction of ticks in an area where ticks were formerly totally eradicated will result in great mortality as the hosts lack natural defence against tick-borne diseases (Jongejan and Uilenberg, 1994)

2.8.4 Pasture spelling

Pasture spelling involves rotating animals into different pastures, with the other pastures left without a host for a period of 6 to 12 weeks or more (Ristic *et al.*, 2012). The period may vary with location, season and type of cattle. Pasture spelling is feasible, when the grazing area is sufficiently large and extra fences and water facilities are available. This method however reduces the stocking rate, thereby affecting the pasture quality. The method is ineffective on species such as *A. variegatum* whose larvae can survive up to 11 months, and adults up to 20 months without feeding (Barré and Uilenberg, 2010). Pasture spelling works in collaboration with chemical control as the host must be treated with an acaricide before being moved into a new pasture and may be incorporated with the use of resistant cattle for an integrated approach of tick control (Ristic *et al.*, 2012).

2.8.5 Habitat modification

Regular bush fires which occur in the dry winter season, burn the tall dry grass which harbour tick larvae and nymphs (Fyumagwa *et al.*, 2007). This results in desiccation of ticks due to unavailability of vegetation cover to shield them from weather elements. The fire also burns ticks if it is a slow hot burn. The eradication of tall grasses results in migration of small vertebrates which are key hosts of immature ticks which are prevalent at this season, therefore reducing the chances of the ticks to successfully find a host to feed on. However, there is great controversy on the extent of harm prescribed fires induce on the veld (Dugmore, 2012). Fires release a lot of carbon dioxide which contribute to global warming. The soil is also destroyed affecting the nutrient content and ability to support plant and animal life. Despite prescribed fires, the veld can be ploughed so as to expose the soil and free-living ticks to the desiccating sun. Mowing can also be done to reduce vegetation height.

2.9 Tick control measures in Zimbabwe

In Zimbabwe, the control of tick and tick-borne diseases has been centred on acaricide use (Perry *et al.*, 1990). Dipping is the main method used, and this has been feasible due to the extensive dipping infrastructure available in the country (Perry *et al.*, 1990). The dipping regime is divided between the public (communal lands) and private sector (commercial farming areas). The Department of Veterinary Services controls and regulates dipping in the communal areas, as well as acquiring the acaricide to use. Amitraz (Triatix[®]) was greatly used as it only required one application on the day of dipping and had a greater residual effect. Dipping is done weekly or fortnightly in summer and attendance of all cattle for dipping enforced. In the commercial farming areas, dipping is totally dependent on the individual farmer. Choice of acaricide type is also dependent on him although the chosen acaricide should be within the gazetted approved acaricides to be used in Zimbabwe.

CHAPTER 3

3 MATERIALS AND METHODS

3.1 Study area

The study was conducted at Imire Game Ranch which is located some 105 km to the east of Harare (Figure 3.1). The ranch lies between latitudes 18° 26' S and 18° 31' S, and longitudes 31° 26' E and 31°32' E. It is at an altitude of 1,300 m above sea level, and covers an area of about 4,500 hectares. The mean annual rainfall is 750 mm, and the climate is characterised by two distinct seasons, namely dry season (April-October) and wet season (November-March). The ranch is dominated by open grasslands, wooded grasslands and open woodlands. Livestock production is integrated with wildlife conservation. The ranch is subdivided into four sections, with one section exclusively reserved for commercial farming and the remainder jointly used for cattle and wildlife ranching. The study was carried out in two wildlife sections as outlined in Figure 3.1.

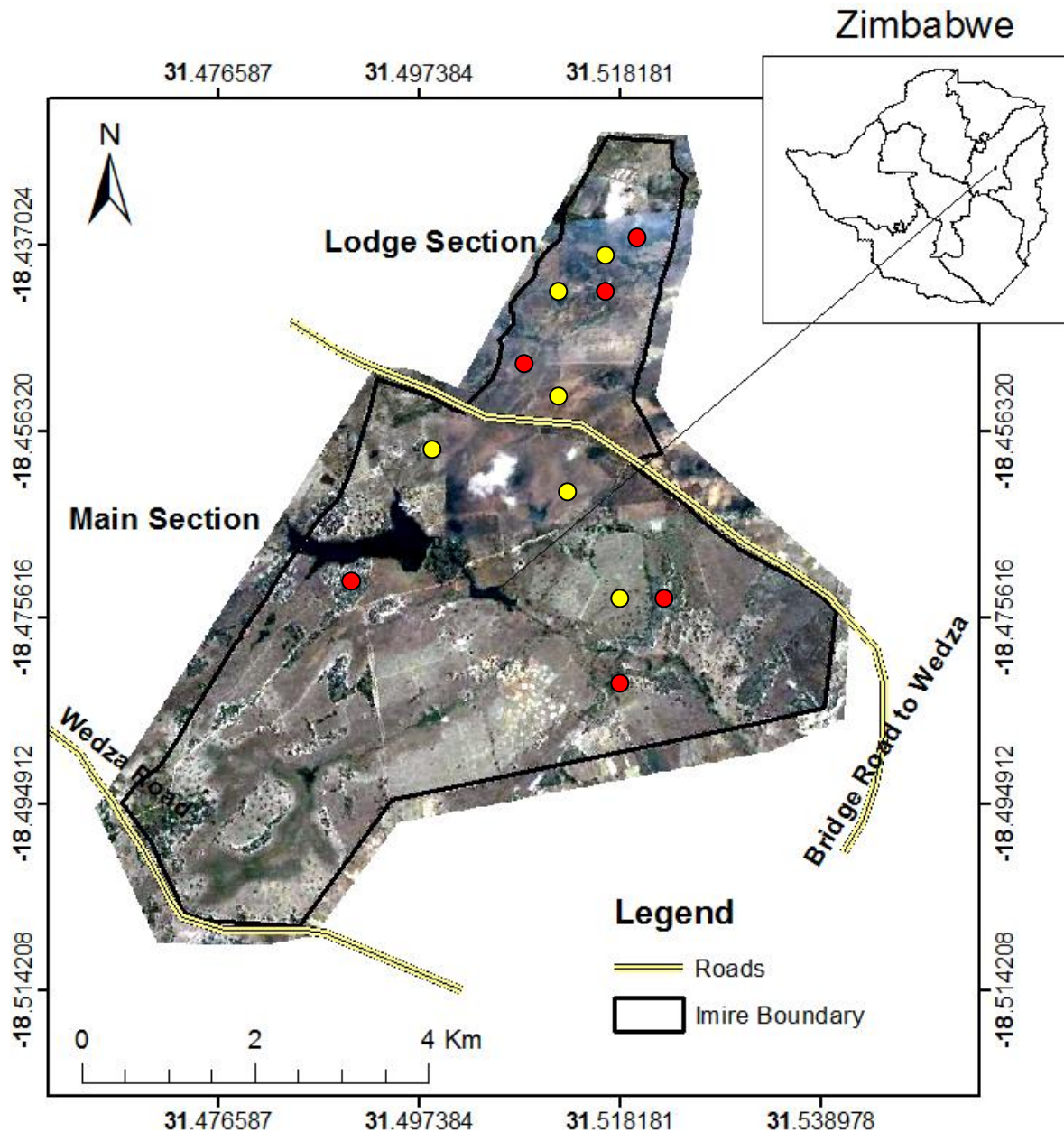


Figure 3.1: Map of Imire Ranch showing the two sections and study sites (yellow:grassland, red:woodland).

3.1.1 Main section

This is a 2,200 hectares section of the ranch that is demarcated by a fence (Figure 3.1). The vegetation of this section is dominated by *Brachystegia spiciformis*, *Julbernadia globiflora*, *Acacia siberiana* and *Acacia nilotica*. Communities of *Combretum molle*, *Dichrostachys cinerea*, *Ziziphus mucronata*, *Lantana camara*, *Peltophorum africanum* are dispersed in the

woodlands. There are *Eucalyptus* plantations in some parts of the section. The grass community comprises of *Hyparrhenia filipendula*, *Sporobolus pyramidalis*, *Craspidorachis africana*, *Digitaria milaniana*, *Pogonarthria squarrosa*, *Loudetia simplex* and *Hypathelia dissoluta*. A number of streams and dams serve as water sources for cattle and wildlife.

Wildlife includes five elephants (*Loxodonta africana*), nine giraffes (*Giraffa camelopardalis*), five black rhino (*Diceros bicornis*), two white rhino (*Ceratotherium simum*), several hundred impalas (*Aepyceros melampus*), unknown number of zebras (*Equus burchelli*), eland (*Oryx gazelle*), sable (*Hippotragus niger*) and blesbok (*Damaliscus dorcus phillipsi*). The section also contains 434 Brahman cattle reared for beef production. The cattle are not herded, but separated into weaners, cows and bulls for controlled breeding. Supplementary feeding is availed in the dry winter period.

3.1.2 Lodge section

The Lodge section covers an area of 1,000 hectares, and is demarcated by a fence (Figure 3.1). Its vegetation is similar to that of the Main section described above. This section includes a river and a dam that provides water for the animals.

Wildlife in this section includes one elephant (*Loxodonta africana*), 31 buffaloes (*Syncerus caffer*), several hundred impalas (*Aepyceros melampus*), one crocodile (*Crocodylus niloticus*), several wildebeest (*Connochaetes taurinus*), kudu (*Tragelaphus strepsiceros*) and warthogs (*Phacochoerus africanus*). This is the only section inhabited by buffaloes. Buffalo act as reservoirs of FMD, which is transmitted to cattle directly or through other species (Bastos *et al.*, 2000). *Theileria parva* is also endemic to buffaloes and transmitted to cattle by *Rhipicephalus appendiculatus*, causing East Coast Fever (Walker *et al.*, 2014). As buffalo are a carrier of diseases that commonly kill cattle, there is total exclusion of cattle in this section

(Schroder *et al.*, 2006). The buffalo are, however, herded and penned at night for security reasons. A rotation system is used which is mainly based on pasture availability.

3.2 The tick management strategy at Imire Ranch

The management at Imire Ranch uses chemical tick control on livestock to regulate tick populations both on the hosts and on the vegetation (free-living) (Horak *et al.*, 1983; Zieger *et al.*, 1998). Chemical tick control is applied on cattle and buffaloes to regulate free-living and parasitic ticks in the ranch. In the main section where wildlife is integrated with cattle production, cattle are used to control free living and parasitic ticks. Four hundred and thirty four cattle freely roam in the main section. These are plunge-dipped after six days in the rainy season and 14 days in the dry season with an acaricide amitraz (Triatix[®], Coopers (Pty) Ltd). However the interval is adjusted in response to the intensity of the tick burden observed on the host on the day of dipping. Only chemical control is used in the ranch.

In the lodge section where cattle are totally excluded, buffaloes are chemically treated with an acaricide similar to that used in the main section. Thirty one buffaloes are herded in this section for six days in the rainy season and 14 days in the dry season before being hand-sprayed with an acaricide similar to that used on cattle in the main section. The spraying interval is also adjusted in response to intensity of the tick burden observed on the buffaloes on the day of spraying. Acaricide application is postponed on rainy days.

3.3 Tick sampling

Tick sampling was conducted in the two sections of the ranch described above. Sampling sites were selected according to vegetation type, namely grassland or woodland, following the proposed tick sampling protocol of Estrada-Peña *et al.* (2013). Three woodland and three grassland communities were randomly selected as the main sampling sites from the Lodge

and Main sections. At each sampling site, three line transects, each 115m long, were systematically laid at an interval of 50 m. Transects were 115 m long to cater for the heavily aggregated spatial distribution of ticks even on homogenous vegetation and under similar weather conditions (Randolph, 2000). Each transect was divided into five sub-transects of 20 m length each, which is the common drag stop distance as recommended by Duik-Waser *et al.* (2006), and interspaced by a 3 m x 3 m quadrant (five quadrats in all) (Figure 3.2). Sampling was conducted along these sub-transects and quadrats. Tick sampling was conducted for three consecutive days each month from March to September 2015 during the third week of the month. Ticks of all stages (larvae, nymphs and adult) were collected in the mid morning and late afternoon. The two sampling methods used are described below.

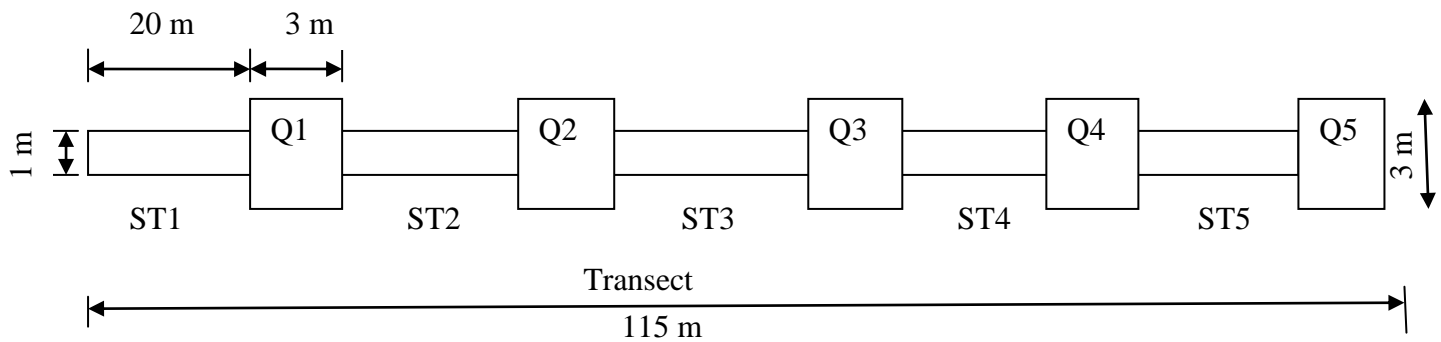


Figure 3.2: Sampling design of each transect used to sample ticks at Imire Ranch (ST: Sub transect, Q: quadrat)

3.3.1 Drag sampling

In each sub-transect (Figure 3.2), ticks were collected by dragging a 1 x 1.25 m white flannel cloth (“flag”) with a dowel rod attached to the anterior end using staples, and a chain hemmed into the posterior end. A rope was attached to the protruding ends of the dowel rod. Ticks were removed after every 20 m distance, which is the common drag stop distance (Diuk-Wasser *et al.*, 2006). All ticks from the same sub-transect that adhered to the cloth

were collected using a pair of forceps and stored in coded vials containing 70% ethanol for later identification.

3.3.2 Visual search method

The Visual Search Method, as described by Terassini *et al.* (2010), was used in each 3 m x 3 m quadrat (Figure 3.2). Questing ticks were searched on tips of grasses, branches and twigs. All questing ticks in the quadrat were collected using a pair of forceps and stored in a container containing 70% alcohol for later identification. The drag method is efficient in collecting immature ticks, while the visual search method is efficient in collecting mature ones (Terassini *et al.*, 2010). Both methods were, therefore, used in order to efficiently sample the ticks. Each sub-transect was paired with a quadrat bordering it i.e. ST1 and Q1 (Figure 3.2), and the collected ticks were stored in the same container with ticks collected by the drag method.

3.3.3 Environmental variables/weather elements

Temperature, humidity, sward height, mat depth and soil moisture were measured in each sub-transect on the day of sampling. Therefore, each variable was measured five times in each transect. The ground temperature was measured using a dry bulb thermometer. The measurement were taken from the middle of each sub-transect. Humidity was measured using a digital hygrometer at the beginning of each sub-transect. Sward height was measured using the direct method as illustrated by Stewart *et al.* (2001) using a clear plastic 30 cm ruler and a tape measure if the sward height exceeded 30 cm. A hand was placed at the height where 80% of the vegetation grew, and the reading taken with a ruler. The mat depth (mm) was measured by pushing a 30 cm clear plastic ruler into the ground until it was met by resistance then recording the depth.

A soil sample was collected from the middle of each sub-transect in order to assess soil moisture. The gravimetric method as described by De Angelis (2007) was used to measure soil moisture. The weight of a labelled dry crucible was measured using a balance with a precision of 0.001 g. The balance was then tarred to reset to zero, and wet soil of 10 g added into the crucible. The soil was then oven dried at 105⁰C overnight. The soil was allowed to cool and reweighed as the mass of dry soil. Soil moisture content (%) was calculated using the formula below:

$$\text{Soil moisture (\%)} = \frac{(M_w - M_d)}{M_d} \times 100$$

Where: M_w = Mass of wet soil sample

M_d = Mass of dry soil sample

3.4 Tick identification

Ticks were identified at the Central Veterinary Laboratory in Harare. Identification and counting of ticks was done under a microscope. All developmental stages were identified to genus level. Nymphs and larvae were only identified to genus level while adult ticks were identified to species level and sexed using identification keys from Walker *et al.* (2003).

3.5 Data analysis

Tick density was not observed for the whole year due to time constraints. However, to better understand temporal variations of tick abundance and composition, the months were grouped according to the season they fall in according to Zimbabwe's climate. Three groups were obtained as follows, hot-wet period (March and April), cold-dry period (May-July) and hot-dry period (August and September). For simplicity and easier understanding, the word season was used in this study to refer to the three groups mentioned above.

A two way non-parametric MANOVA was used to analyse the factors tick sweeper and habitat type; and tick sweeper and season on tick abundance and composition. The Euclidean distance measure was used on non-parametric MANOVA. Discriminant analysis was done on habitats to assess habitat heterogeneity using Statistica software package. Cluster analysis was also done to determine if different tick species preferred the same habitat (habitat preference). A two independent t-test was done on gender to assess if male ticks significantly differed in abundance. Chi-square tests were done to assess if gender significantly differed with season, habitat type and sweeper type using Statistica software package. One way ANOVA was used to assess if abundance of the different tick developmental ages/stages differed at Imire Ranch for the sampled period. Chi square tests were done to assess if tick developmental stages differed with habitat type, season and sweeper type using Statistica software package. A correlation analysis was done to assess the relationship between the environmental variables and tick density. Canonical correspondence analysis was used to assess interaction between environmental variables and tick composition. The preferred environmental conditions for each tick species and age was also determined. All other analyses were done using PAST software package and judged at a 95% confidence level.

CHAPTER 4

4 RESULTS

4.1 Tick abundance and species diversity at Imire Ranch

A total of 5,124 ticks with a mean density of 4.06 ticks/29 m² were collected during the seven months sampled, in the two sections of Imire Game Ranch (Table 4.1).

Table 4.1: Ticks recorded in the two sections at Imire Ranch. [N = Number of ticks recorded, D = Density (ticks/29 m²) and C = Composition of ticks (%)]

Tick life stages	Main/cattle-swept Section			Lodge/buffalo-swept Section			TOTAL		
	N	D	C	N	D	C	N	D	C
Adults									
<i>Rhipicephalus appendiculatus</i>	97	0.154	93.27	1732	2.749	99.08	1829	1.45	98.76
<i>Rhipicephalus evertsi</i>	5	0.008	4.81	12	0.019	0.69	17	0.01	0.92
<i>Haemaphysalis leachi</i>	2	0.003	1.92	1	0.002	0.06	3	0.00	0.16
<i>Hyalomma truncatum</i>	0	0.000	0.00	1	0.002	0.06	1	0.00	0.05
<i>Hyalomma rufipes</i>	0	0.000	0.00	2	0.003	0.11	2	0.00	0.11
Adult total	104	0.165		1748	2.775		1852	1.46	
Immatures									
<i>Rhipicephalus larvae</i>	521	0.827	61.29	1763	2.798	41.25	2284	1.81	44.57
<i>Rhipicephalus nymph</i>	224	0.356	26.35	763	1.211	17.85	987	0.78	19.26
<i>Amblyomma larvae</i>	1	0.002	0.12	0	0.000	0.00	1	0.00	0.02
TOTAL	850	1.349	16.59	4274	6.784	83.41	5124	4.07	

R. appendiculatus was the most dominant tick species; comprising 98.8% of adult ticks captured in the area, followed by *R. evertsi*, *H. leachi*, *H. truncatum* and *H. rufipes* making up 0.92%, 0.16%, 0.05% and 0.11%, respectively. Larvae were recorded in two genera, *Rhipicephalus* and *Amblyomma*, with *Rhipicephalus* being dominant. *Rhipicephalus* was the only one collected at nymph stage. Immature ticks in the genus *Rhipicephalus* however may have been mainly composed of *R. appendiculatus* as it was the dominant species.

4.2 Efficacy of the two tick sweepers

4.2.1 Effect of season and tick sweeper

The buffalo-swept section had a higher tick abundance of 4274 and density of 6.78 ticks/29 m² compared to the cattle-swept section's 850 and density of 1.34 ticks/29 m² (Table 4.1). This difference was significant ($F = 28.944$, $P = 0.0001$). The buffalo-swept section recorded a higher species richness of 5 compared to 3 in the cattle swept section (Table 4.1). It, however, contained lower tick diversity and evenness ($1-D = 0.06$, $E = 0.21$) as compared to the cattle swept section ($1-D = 0.29$, $E = 0.44$). There was a significant effect of season on tick composition and abundance ($F = 10.298$, $P = 0.0001$), with adult ticks being more abundant in the hot-wet season, while larvae dominated in the hot dry season (Figure 4.1). There was no interaction between the effect of season and control regime on tick density and composition ($F = 16.286$, $P = 0.2307$) (Figure 4.2). However, the hot-wet season had the highest density in the buffalo controlled area while the hot-dry season showed the highest density in the cattle-swept area. The lowest density was observed in the hot-wet and cold-dry season for the cattle swept and buffalo-swept areas respectively.

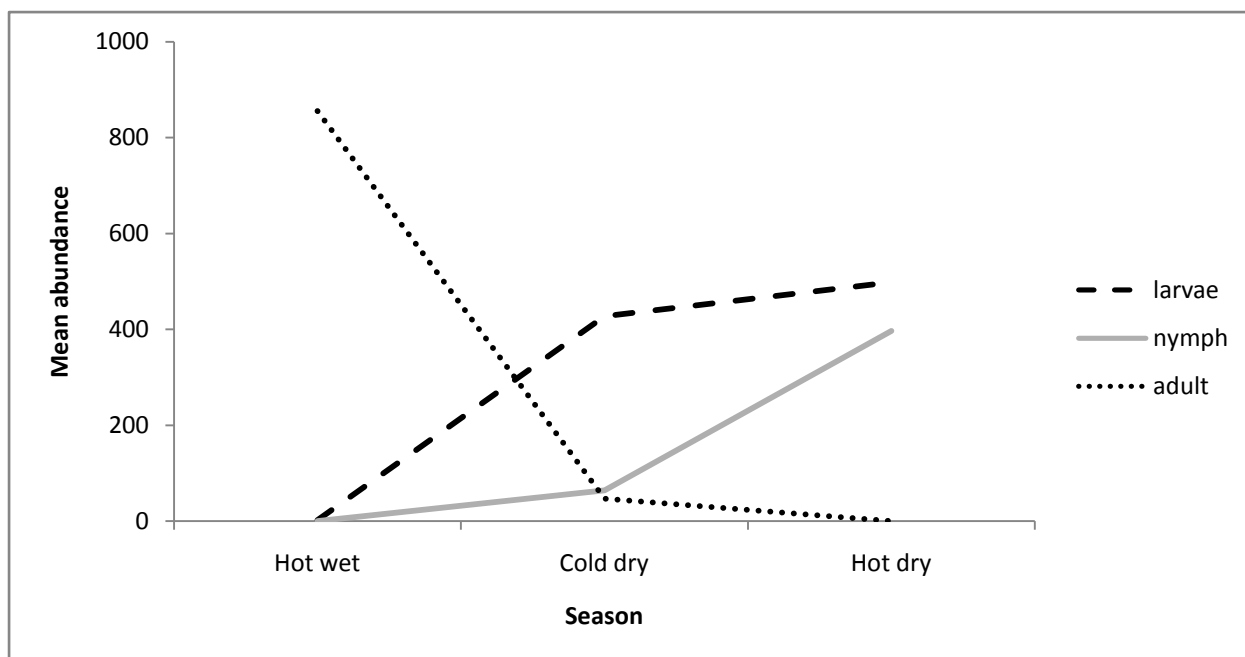


Figure 4.1: Mean abundance of different tick developmental stages across seasons

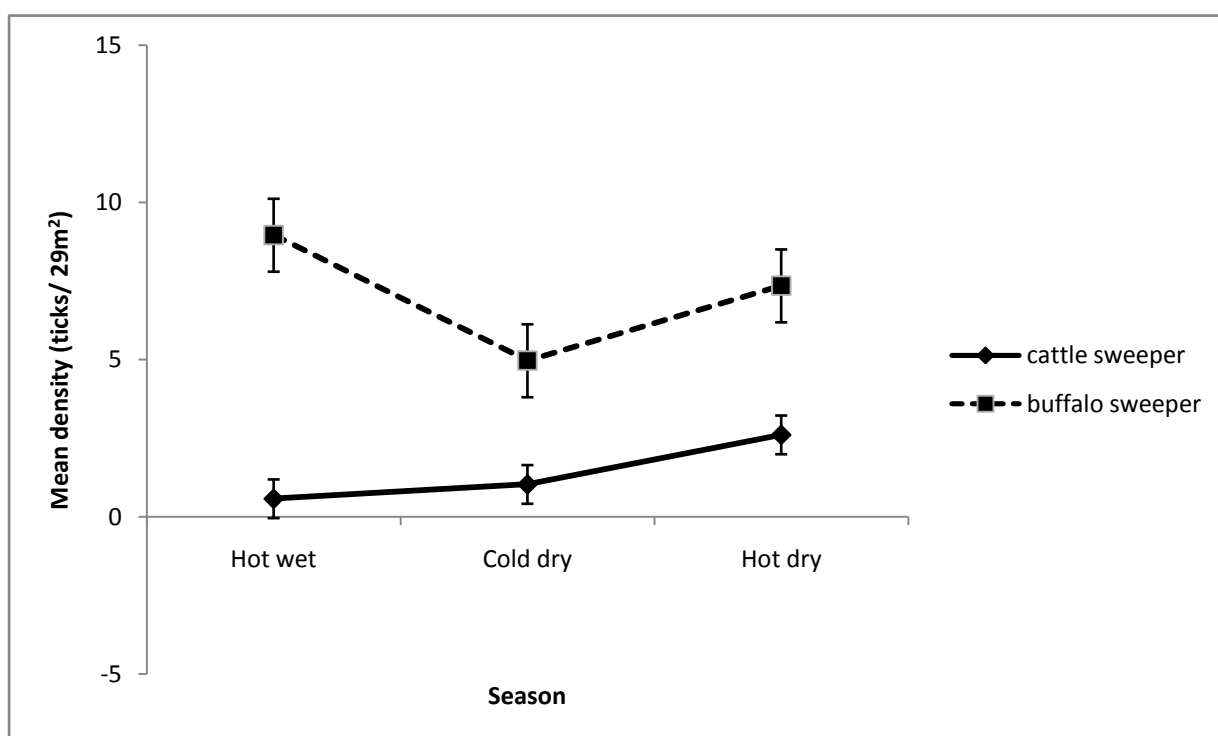


Figure 4.2: Seasonal mean tick densities in cattle and buffalo swept sections

4.2.2 Tick sweeper and habitat

There was a significant difference in efficacy of the two tick sweepers used in the different sections at Imire Game Ranch ($F = 28.224$, $P = 0.0001$), with the buffalo swept section having a higher abundance in both habitats (Figure 4.3). Tick density and composition in the two habitats was also significantly different ($F = 7.334$, $P = 0.007$), with woodlands composed of a higher abundance (Table 4.2). There was an interaction between the effect of tick sweeper and habitat type ($F = 11.288$, $P = 0.001$). There was a marked increase in tick abundance in the buffalo-swept area as habitat changed from grassland to woodland while a small reduction in abundance was observed in the cattle-swept area.

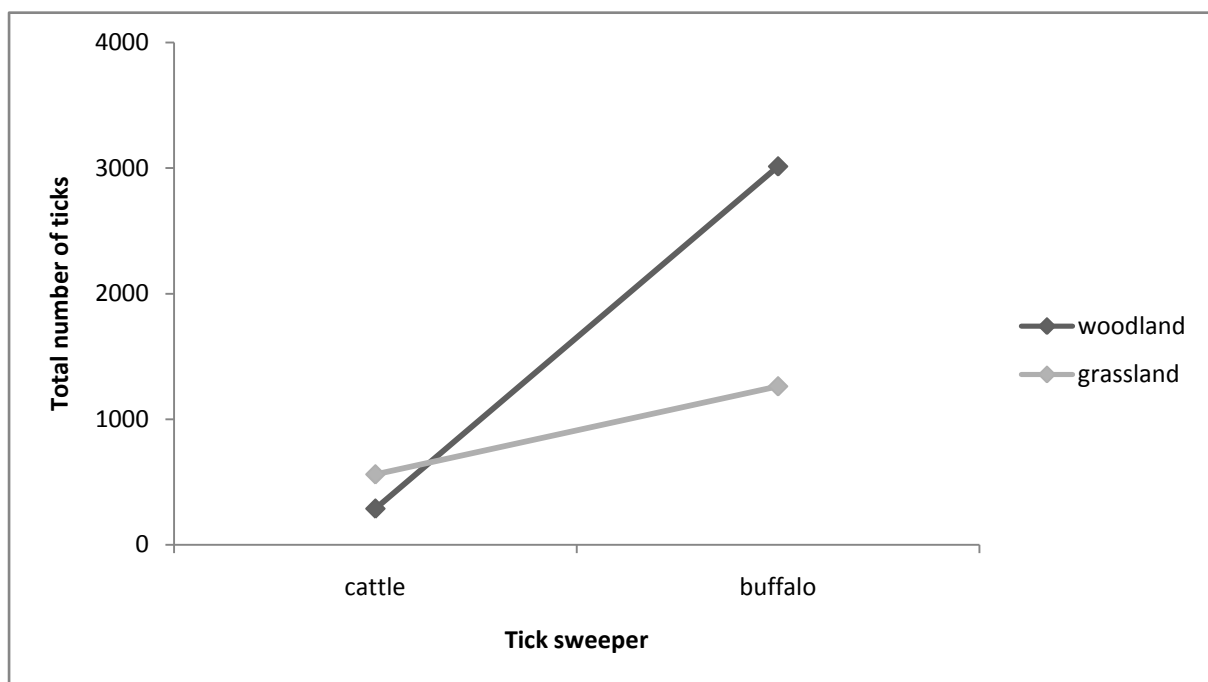


Figure 4.3: Total number of ticks in woodlands and grasslands in relation to sweeper type

Table 4.2: Total number of ticks (adults and immatures combined) in each habitat and section

Section	Woodland	Grassland	Row totals
Main	289	561	850
Lodge	3,013	1,261	4,274
Column totals	3,302	1,822	5,124

4.3 Species habitat preference

Discriminant analysis showed that the two habitats were significantly different in species composition and abundance ($F = 2.688631$, $P < 0.0062$). Ninety-three percent of grasslands were correctly classified while only 13% of woodlands were correctly classified (Table 4.3). The habitats were classified in relation to tick density with woodlands being sites with high *R. appendiculatus* and *Rhipicephalus* larvae and nymph densities. Only 6.5% of grassland quadrats/sites had high abundances to be misclassified as woodlands and about 87% of woodland quadrats/sites misclassified as grasslands. The majority of the misclassified woodlands were observed in the Main section (301 quadrats/sites). Misclassified grassland sites were sites close to a dam while others had a sward height above 65cm.

Table 4.3: Discriminate classification matrix of habitats

Habitat	% correctly classified	Grassland	Woodland
Grassland	93.49	589	41
Woodland	13.17	547	83
Total	53.33	1,136	124

Rows: observed classification

Column: predicted classifications

Cluster analysis at a linkage distance of 60, grouped the species into four clusters, with *R. appendiculatus* very dissimilar from the other species (Figure 4.4). *R. appendiculatus* did not associate itself with other species and developmental stages. The two immature stages of the genus *Rhipicephalus* were also dissimilar. The other species and developmental stages associated into one group. It should be noted that all species names were for adult tick stages with genus names for the other developmental stages.

4.4 Developmental stage

Abundances of the different tick developmental stages (larva, nymph and adult) significantly differed ($F = 4.411$, $P = 0.0122$), although larvae and nymphs were the only stages significantly different (Figure 4.5). Nymphs were about half the number of larvae.

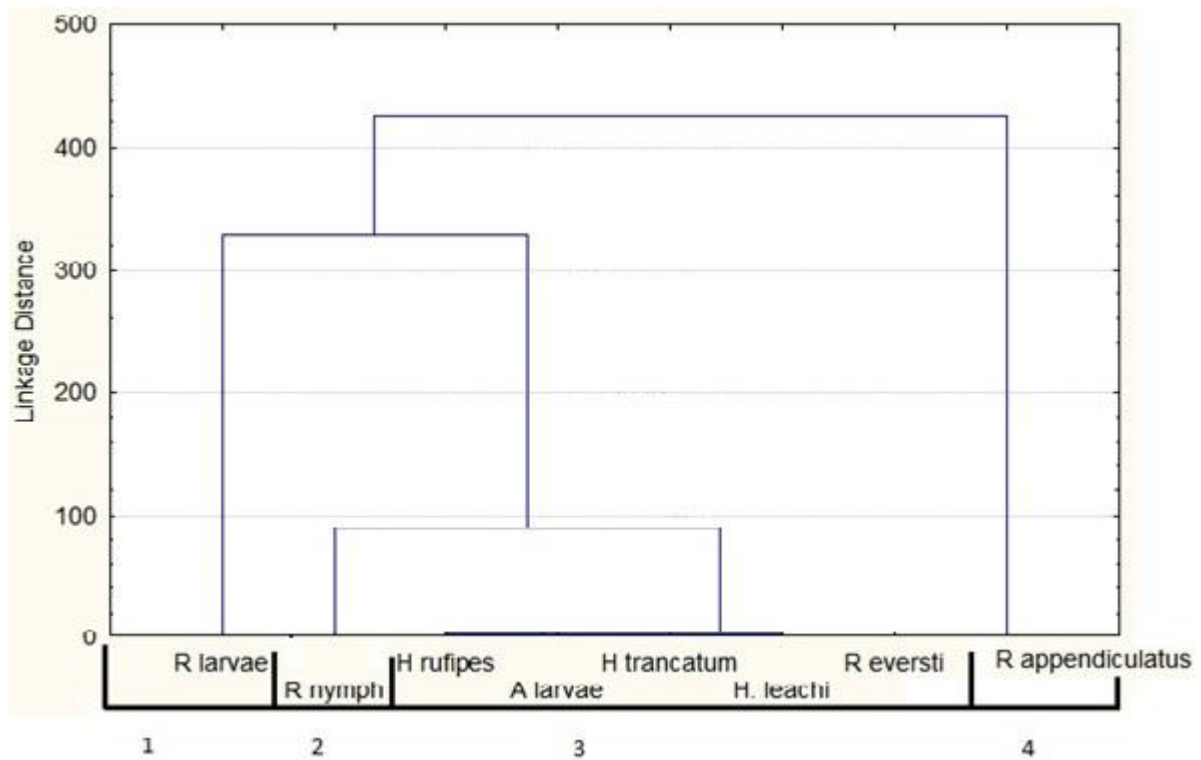


Figure 4.4: Cluster analyses of adult tick species and immature tick genus found at Imire Ranch

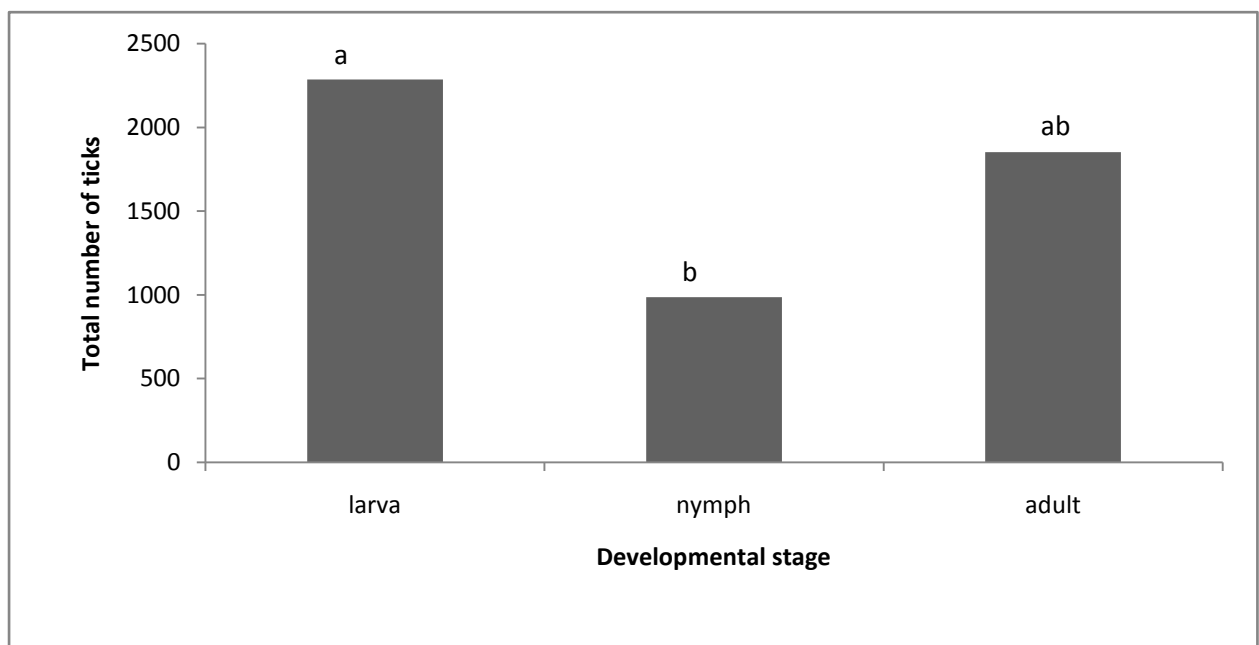


Figure 4.5: Total number of ticks in each developmental stage. Different lowercase letters indicate differences which are statistically significant ($P < 0.05$)

Tick developmental stage significantly differed with season ($\chi^2 = 5109.301$, $df = 8$, $P < 0.05$) (Figure 4.1). Adults were dominant in the hot-wet season, while larvae were highest in the cold-dry season. Larvae and nymphs co-dominated in the hot-dry season. Mean monthly abundance of larvae and nymphs increased as season progressed from hot-wet to hot-dry while adults decreased. However mean larval abundance was highest in both cold and hot-dry seasons.

Tick developmental stages significantly differed with sweeper type ($\chi^2 = 252.392$, $df = 5$, $P < 0.05$) (Figure 4.6). Adults and larvae co-dominated in the buffalo-swept section with nymphs having the least abundance. A change in sweeper type to cattle resulted in a dominance of larvae, with adults being the least abundant. More ticks at all developmental stages were however recorded within the buffalo swept section than in the cattle swept section. Tick developmental stages significantly differed with habitat ($\chi^2 = 757.4516$, $df = 5$, $P < 0.05$) (Figure 4.7). Adults were the highest in woodlands, but became the lowest in grasslands, while the second abundant larvae in the former became the most abundant in the latter.

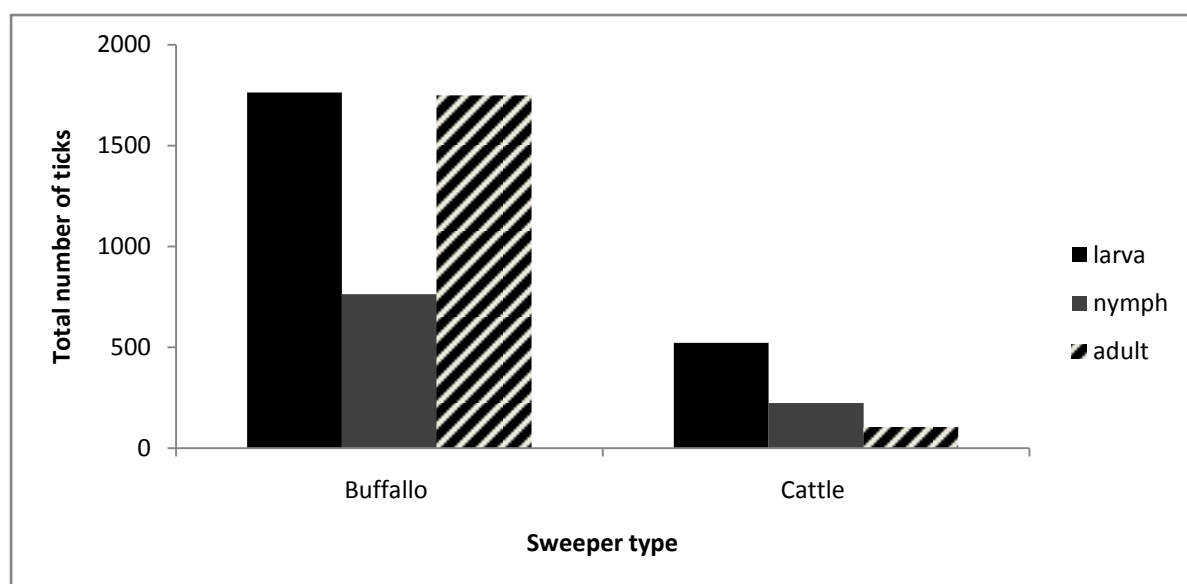


Figure 4.6: Total number of ticks in each developmental stage according to sweeper type

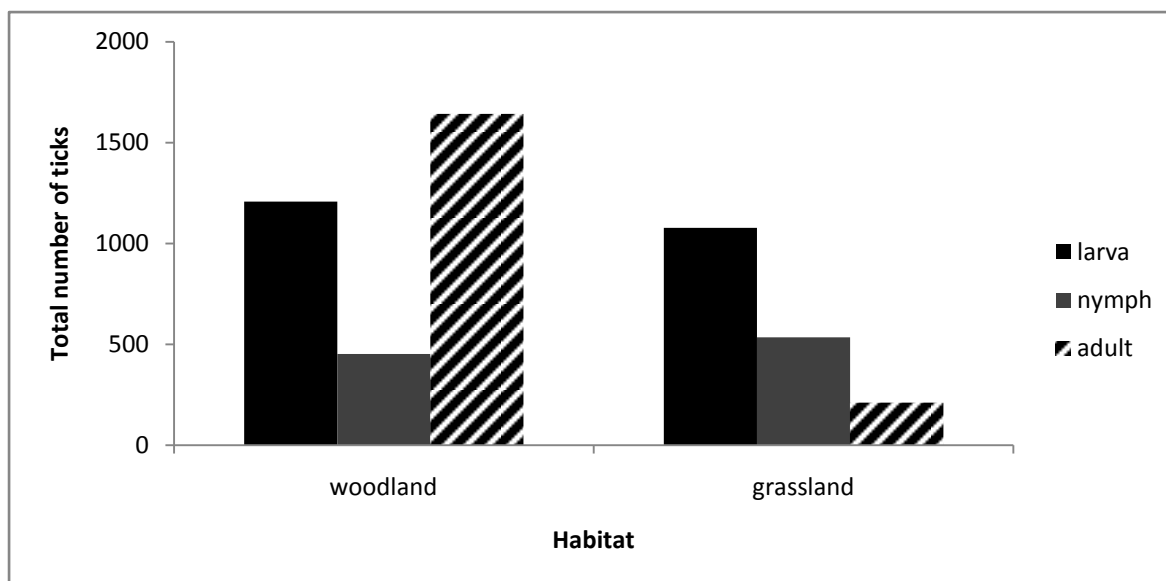


Figure 4.7: Total number of ticks in each developmental stage according to habitat

4.5 Gender

The total number of female ticks was more than that of male ticks, irrespective of species (Figure 4.8). However, this difference was not significant ($T = -0.44297$, $P = 0.6578$).

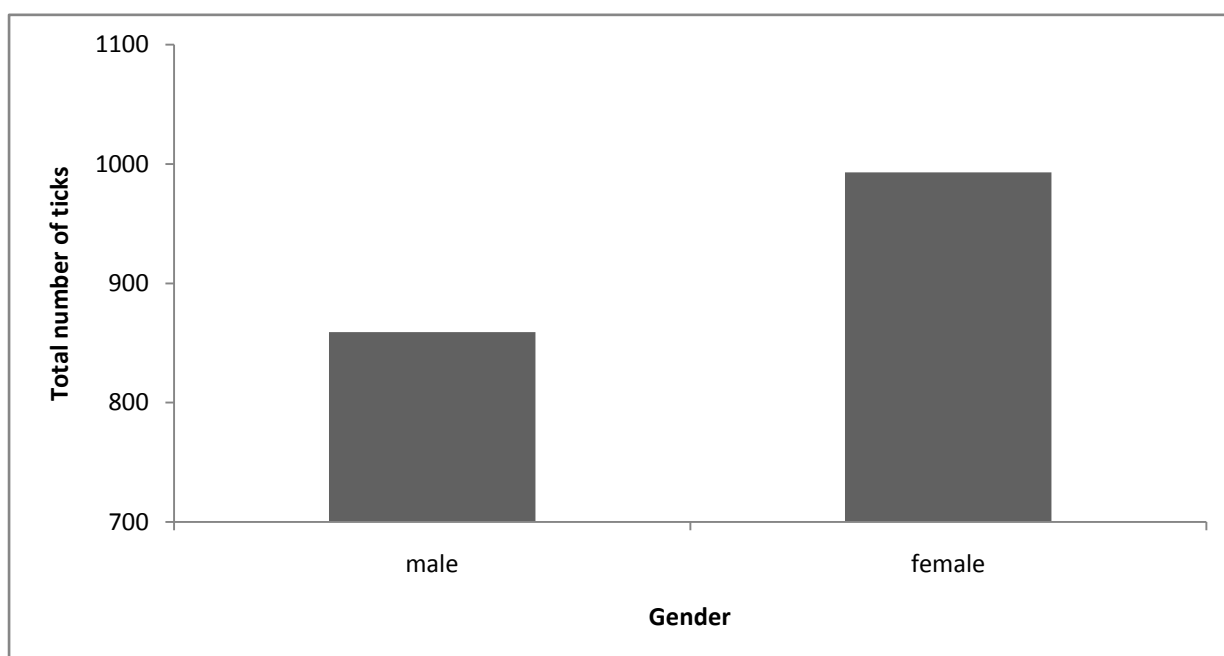


Figure 4.8: Total tick abundance of male and female ticks at Imire Ranch

Gender was not significantly different with tick sweeper ($\chi^2 = 0.205091$, $df = 3$, $P = 0.98656$) (Figure 4.9). Both sweeper types resulted in a female dominance although it was greater in the cattle swept area.

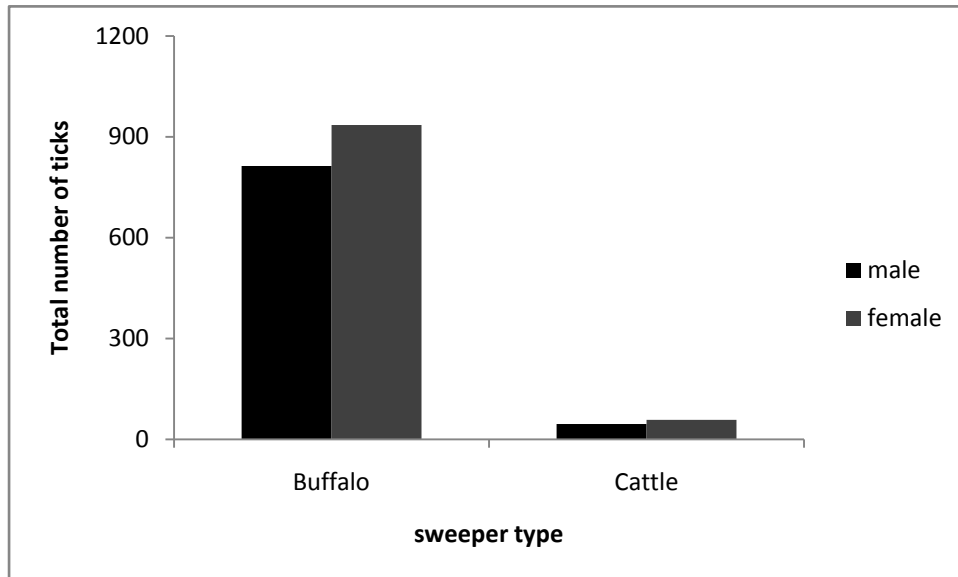


Figure 4.9: Total number of ticks in each gender across sweeper types

Gender was not significantly different with season ($\chi^2 = 0.899793$, $df = 5$, $P = 0.970236$), with both the hot-wet season and cold-dry season showing a female tick dominance (Figure 4.10). There was no significant difference in gender with habitat type ($\chi^2 = 0.279457$, $df = 3$, $P = 0.963844$) (Figure 4.11), with both habitats characterised by a female tick dominance (Figure 4.11)

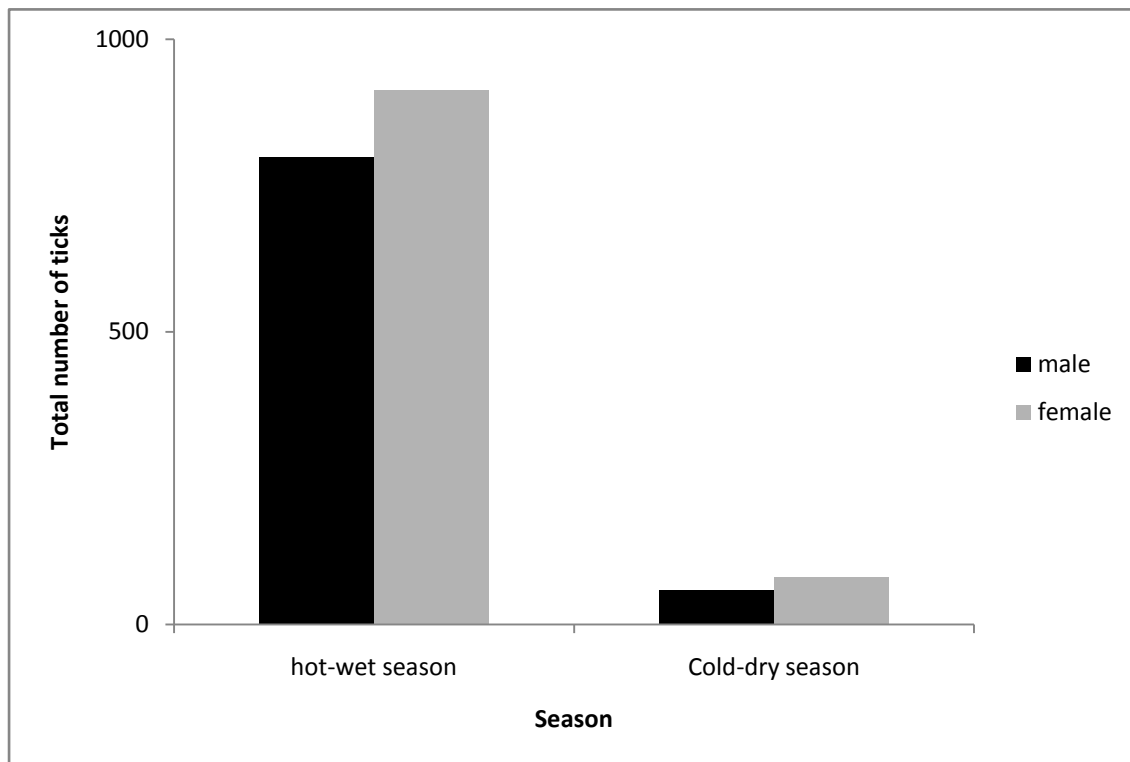


Figure 4.10: Total number of ticks in each gender across seasons

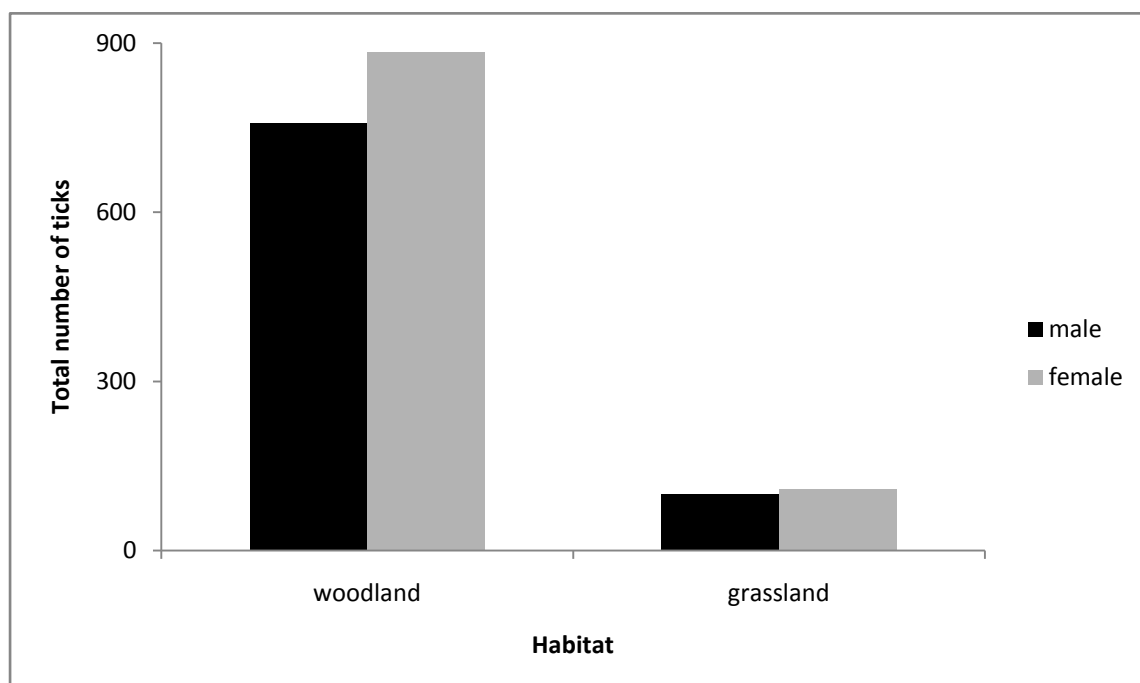


Figure 4.11: Total number of ticks in each gender across habitats

4.5.1 Sex ratio of tick species

R. appendiculatus was the only species with sufficient numbers to investigate sex ratio. Therefore, other species were omitted in this study. *R. appendiculatus* had higher numbers of females than males in both the Main and Lodge Section (Table 4.4). Although both sweeper types induced a female dominance, the cattle sweeper resulted in a greater female dominance.

Table 4.4: *R. appendiculatus*'s sex ratio and abundance of male and female ticks in the cattle and buffalo swept areas at Imire Ranch

Sweeper type	Abundance		Ratio
	Male	Female	Male: female
Cattle	43	54	1: 1.3
Buffalo	802	930	1: 1.2
Total	845	984	1:1.2

R. appendiculatus exhibited a female dominance in the hot-wet and cold-dry season (Table 4.5). There was a variation in the sex ratio with season, with an increase in the sex ratio as the season progressed from the hot-wet to the cold-dry season. *R. appendiculatus* had more females than males in both habitats although woodlands had a higher female oriented sex ratio as compared to grasslands (Table 4.6).

Table 4.5: *R. appendiculatus*'s sex ratio and abundance of male and female ticks in the hot-wet and cold-dry season at Imire Ranch

Season	Abundance		Sex ratio
	Male	Female	Male: female
Hot-wet	790	905	1: 1.2
Cold-dry	55	79	1: 1.4
Total	845	984	1: 1.2

Table 4.6: *R. appendiculatus*'s sex ratio and abundance of male and female ticks in grasslands and woodlands at Imire Ranch

Habitat	Abundance		Sex ratio
	Male	Female	Male: female
Grassland	99	108	1: 1.1
Woodland	746	876	1: 1.2
Total	845	984	1: 1.2

4.6 Environmental variables

Tick density was greatest at temperatures between 21-30°C with lower densities at temperatures above or below this temperature range (Table 4.7). However, the lowest temperature recorded was 12°C and the maximum being 45°C. There was no linear correlation between temperature and tick density ($r = 0.05$, $P > 0.05$) (Table 4.8). Tick density increased with an increase in sward height, but started to reduce when sward height exceeded 80 cm. There was a significant weak positive linear correlation between sward height and tick density ($r = 0.13$, $P < 0.05$). Tick density was greatest at a mat depth of between 31-40 mm. A mat depth of 21-30 mm had the lowest density of 1.1 ticks/ 29 m².

Table 4.7: Tick density with variation in environmental variables at Imire Ranch

Environmental variable	Range	Mean density (ticks/29 m²)
Temperature (°C)	10-20	1.6
	21-30	5.1
	31-40	3.9
	41-50	2
Sward height (cm)	0-20	2.1
	21-40	3.1
	41-60	4.8
	61-80	10.1
	81-100	8.5
	100-120	0.6
Mat depth (mm)	0-10	4
	11-20	8.4
	21-30	1.1
	31-40	8.5
	41-50	8
Soil moisture (%)	0-20	4.1
	21-40	3
	41-60	0.3
	61-80	0
	above 80	0
Humidity (%)	0-20	3.7
	21-40	4.4
	41-60	4.2
	61-80	2.4

There was no linear correlation between mat depth and tick density ($r = 0.01$, $P > 0.05$). High tick densities were observed at low soil moisture with a reduction in tick density as soil moisture increased. However, there was no linear negative correlation between soil moisture

and tick density ($r = -0.05$, $P > 0.05$). Tick density increased as humidity increased but ceased to increase beyond 40%. Tick density reduced beyond 40% humidity. No humidity was recorded which was above 80%. There was no correlation between humidity and tick density ($r = -0.02$, $P > 0.05$).

Table 4.8: Correlation coefficient values of environmental variables with tick density

Environmental variable	Correlation coefficient (r)	p value
Soil moisture	-0.05	0.08
Humidity	-0.02	0.46
Temperature	0.05	0.06
Height	0.13	2.92E-06
Mat depth	0.01	8.53E-01

Rhipicephalus larvae were more abundant on sites with high sward height and high soil moisture while *Rhipicephalus* nymph associated itself with high humidity (Figure 4.12). All adult species preferred sites with high mat depth and low temperature. However *R. evertsi* and *R. appendiculatus* differed from the other adult species as they preferred higher humidity.

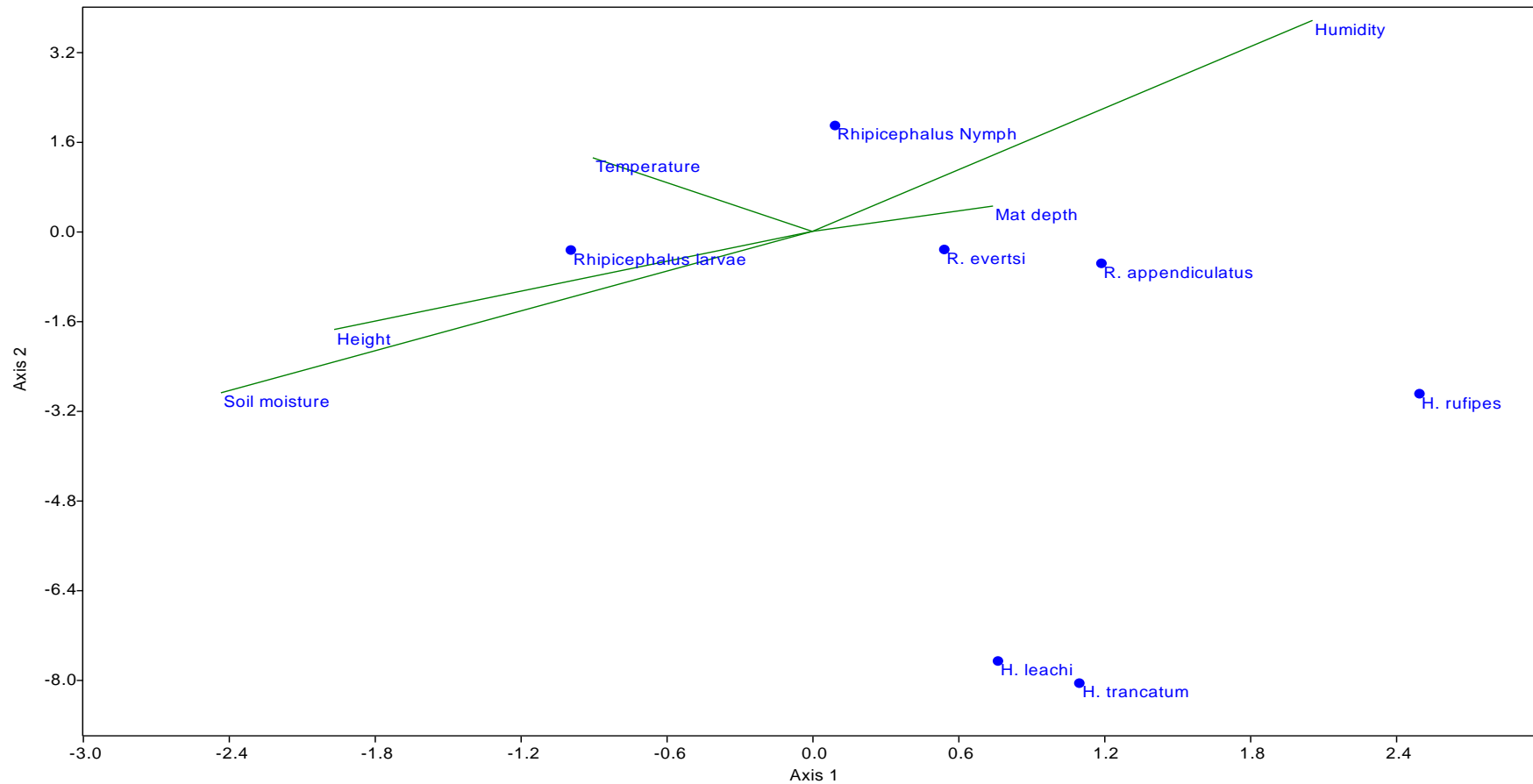


Figure 4.12: Canonical correspondence output of interaction between tick species and environmental factors (humidity, temperature, soil moisture, sward height and mat depth)

CHAPTER 5

5 DISCUSSION

5.1 Tick abundance and species diversity at Imire Ranch

The present study recorded some 5,124 ticks within Imire Ranch. The ticks included all developmental stages, with five species identified at adult stage. Although the five belonged to the genera *Hyalomma*, *Rhipicephalus* and *Haemaphysalis*, only *Rhipicephalus*, was observed at nymphal stage. The genus *Hyalomma* which is represented by *H. truncatum* and *H. rufipes* in Zimbabwe, have no questing nymphal stages as both species are two-host tick species (Walker *et al.*, 2003). The genus *Haemaphysalis*, represented by *Haemaphysalis leachi* primarily feeds on dogs and wild carnivores (Walker *et al.*, 2003), but as wild carnivores are kept in cages at Imire Ranch and tick distribution is influenced by availability of preferred hosts (Tonnesen *et al.*, 2004), the life stages of this species are only likely to be observable within the enclosures. This explains the presence of a single genus at nymphal stage. All collected *Rhipicephalus* nymphs are likely to belong to *R. appendiculatus* as *R. evertsi* (the other *Rhipicephalus* species collected) is a two host tick species (Walker *et al.*, 2003).

Genus *Amblyomma* was only collected at larval stage as it is the only developmental stage that quest, while other stages are active hunters (Walker *et al.*, 2003; Uys *et al.*, 2015). Thus the drag sampling method is likely to miss ticks at other developmental stages, hence recording an underestimate of populations of both nymphal and adult stages.

Woodlands and grasslands differed in tick composition, with *R. appendiculatus* preferring woodlands (Walker *et al.*, 2003; Schroder *et al.*, 2006). The immature stages of genus *Rhipicephalus* which is mostly composed of the dominant *R. appendiculatus* also preferred

woodlands. Some grassland sites, however, also exhibited high abundances of *R. appendiculatus* and immature stages of genus *Rhipicephalus*. These sites were very close to permanent water sources where high host numbers frequented in search of water. These areas are likely to have high levels of host kairomones which attract ticks (Carroll, 1998; Terassini *et al.*, 2010), thereby resulting in high records of tick densities. De Garine-Wichatitsky *et al.* (1999) also recorded high tick densities at sites close to permanent water sources.

R. appendiculatus was not associated with any of the other species. It appears that this dominant species out-competes and excludes all other species in its preferred habitat (Ghosh and Tsutsui, 2012). The different developmental stages of genus *Rhipicephalus* however, appear to have evolved the capacity to occupy the same niche, in different seasons, with adults, nymph and larvae dominant in the hot wet, hot dry and cold dry seasons, respectively (Latif *et al.*, 2001). The other species, in all developmental stages, occupy separate niches from that of *R. appendiculatus*.

5.2 Efficacy of the tick control regime at Imire Ranch

Although the use of acaricide treated cattle to control free-living ticks shows high efficacy (Zieger *et al.*, 1998), the same cannot be said of acaricide treated buffalo. The low efficacy of the buffalo treatment is attributed to the smaller buffalo herd used at Imire Ranch. On average, each buffalo accounts for 32.26 hectares, whereas each cattle accounts for 5.07 hectares when each animal is related to grazing area. Some of the ticks are host-specific, but host susceptibility to tick infestation is the primary determinant of tick infestation patterns (Gallivan and Horak, 1997). Buffaloes are less susceptible to tick infestation as compared to cattle (Muhammad *et al.*, 2008). This makes them less efficient sweepers, especially in woodlands and in the wet season when tick loads are high. Feeding ticks excrete attraction–aggregation–attachment pheromones which attract unfed/questing ticks to a tick-infested

host. This induces them to aggregate and attach to that particular host (Sonenshine, 2004). This infestation pattern further increases tick loads on cattle, thereby making them better sweepers than buffaloes.

As buffaloes are more resistant to tick infestation than cattle, they are not as efficient as cattle in controlling all tick developmental stages especially the most dominant developmental stages which are larvae and adults. The cattle sweeper resulted in a marked reduction in adult ticks but larval populations dominated this area due to inefficiency of this sweeper type in controlling larval stages as observed by Keesing *et al.* (2013). Preferred questing height of larvae, nymphs and adults differs; with *R. appendiculatus*'s above mentioned stages preferring 26 cm, 31 cm and 70 cm, respectively (Gallivan and Horak, 1997). Host size of ungulates, which relates to its height (Gallivan and Horak, 1997), determines the predominant infesting stage. Immature ticks are only able to reach the bodies of small animals and legs of large ungulates, while adults only reach the bodies of large animals as small animals such as rodents pass below their questing height. Cattle, being large ungulates, may only have a small proportion of larval ticks attaching to them. Hence, they are inefficient sweepers for this developmental stage. This resulted in high tick loads within the Main Section during the cold-dry and hot-dry seasons, as these seasons are dominated by larval stages.

Immature ticks do not significantly affect weight gain in cattle (Gallivan and Horak, 1997). Hence, dipping intervals at Imire Ranch are increased in the cold season and even further extended in the hot dry season so as to reduce costs on acaricide. Walker *et al.* (2014) noted that increased frequency of acaricide application significantly reduced tick loads. In Main Section, lowest tick density was recorded in the hot-wet season as frequency of acaricide treatment was highest. The highest tick density was recorded in the hot-dry season, reflecting the most infrequent acaricide treatment. This management practice, however, results in a built

up of immature ticks during the dry season which is latter followed by an explosion of adult tick populations at the onset of the rainy season.

5.3 Spatial variation in tick abundance at Imire Ranch

Differences in tick abundance and density between the two sections at Imire Ranch, is largely determined by the type of tick sweeper. The more efficient cattle sweeper significantly reduced tick numbers at each developmental stage within Main Section compared to Lodge Section where buffaloes act as sweepers. In addition, the high level of disturbance associated with large numbers of acaricide treated cattle reduced species richness in the Main Section when compared to the moderately disturbed Lodge Section (Haddad *et al.*, 2008). Tick diversity within Lodge Section was however lower than that of Main Section as it was predominantly dominated by a single species, *R. appendiculatus* which accounted for 99% of the total tick population in this part of the ranch.

The dominance of *R. appendiculatus* at Imire Ranch collaborates the observation of Sungirirai *et al.* (2015) who noted its dominance in Natural Farming Region II of Zimbabwe within which Imire Ranch falls. *R. evertsi* was the second dominant tick species as already noted by De Garine-Wichatitsky *et al.* (1999). *Hyalomma* species were rare and only recorded in April, which is at the end of the wet season. This happens to be the period when *R. appendiculatus* goes into diapause (Randolph, 2000), thereby freeing ecological space for *Hyalomma* species. *H. leachi* also known as the yellow dog tick, is prevalent in areas inhabited by dogs (Sungirirai *et al.*, 2015). Dogs are secluded from Imire Ranch. The only dogs that infrequently roam the range belong to the owner of the ranch, but only do so under close monitoring from the owner. This explains the rare occurrence of this species in Imire Ranch. *H. leachi* also primarily feeds on wild carnivores such as big cats, foxes, jackals and

wild dogs (Walker *et al.*, 2003). This accounts for a higher abundance of this species within Main Section where carnivores are kept in cages.

A. hebraeum and *A. variegatum* are the only *Amblyomma* species recorded in Southern Africa (Walker *et al.*, 2003). In Zimbabwe, *A. hebraeum* was originally confined to the Southern districts, but is now spreading northwards due to animal movement associated with land resettlement exercises (Sungirirai *et al.*, 2015). Likewise, *A. variegatum* which was formerly restricted to the north-western part of the country and areas along the eastern border (Hove *et al.*, 2008), was recently recorded in Mazowe (Sungirirai *et al.*, 2015). These two *Amblyomma* species have never been recorded at Imire Ranch and the present record of *Amblyomma* larvae in the ranch is attributed to animal immigration from areas where the species are currently known to occur (Sungirirai *et al.*, 2015). With the dominance of *R. appendiculatus* in Imire Ranch, *Amblyomma* numbers have so far remained low. The single encounter of *Amblyomma* larva made in the current study could indicate high competition from *R. appendiculatus* and failure to thrive under Imire Ranch's environmental conditions (see Cumming, 1999; Estrada-Peña and Salman, 2013).

Vegetation influences the microclimate and abundance of hosts, thus determining tick abundance and activity (Estrada-Peña *et al.*, 2013). In the present study, woodlands were observed as harbouring greater tick abundance than grasslands with adult and larval ticks mostly abundant in this habitat. This collaborates observations made by Schroder *et al.* (2006) and is attributed to the buffering effect of trees from weather extremes, thereby reducing variation in temperature and humidity when compared to conditions under open grasslands (Lindstrom and Jaenson, 2003). The dominant *R. appendiculatus* prefers woodlands over grasslands, thus accounting for the higher abundance in the former (Walker *et al.*, 2003; Schroder *et al.*, 2006). Tick distribution is also influenced by host availability (Estrada-Peña *et al.*, 2013). Main Section is greatly dominated by grazers, thereby

influencing greater abundance of ticks within the grass dominated communities, as engorged adults are likely to be dropping off from hosts within grasslands.

5.4 Temporal variation in tick abundance at Imire Ranch

There were significant seasonal differences in tick density and composition. This is in agreement with the review by Estrada-Peña *et al.* (2013). There were two seasonal peaks in tick abundance, with one in the hot-wet season as also observed by Schroder *et al.* (2006). The second peak was in the hot-dry season. This latter peak is attributed to the combination of hatched larvae and nymph recruitment from moulted larvae at the end of the cold season. Among the three seasons covered in the sampling period, the cold-dry season had the lowest tick abundance. This observation is supported by Swai *et al.* (2006).

Tick questing activity in temperate areas follows changes in photoperiod as it influences tick behavioural and developmental diapause (Estrada-Peña *et al.*, 2013). Tick abundance, therefore, changes with season, with adults, larvae and nymphs being most abundant in the hot-wet, cold-dry and hot-dry season, respectively (Latif *et al.*, 2001). This seasonal pattern of occurrence is instigated by unfed adults which enter behavioural diapause at the end of the wet season by detecting changes in the photoperiod and only breaking their diapause when rains commence (Walker *et al.*, 2003; Estrada-Peña *et al.*, 2013). Unfed adult ticks do not quest at the onset of winter. This results in reduced adult tick loads in winter. This behavioural pattern enables ticks to feed and moult before harsh environmental conditions commence in winter. Thus, no adult ticks were recorded in the hot dry season in accordance with observations by Mooring *et al.* (1994), as unfed ticks undergo diapause (Randolph, 2004). Adult questing behaviour is also thought to be activated by soil humidity which is influenced by rainfall (Stachurski, 2006). The dry, conditions coupled with the hot temperatures, induce diapause in all adult ticks.

The difference in tick surface area to volume ratio results in immature ticks becoming highly susceptible to desiccation (Randolph and Storey, 1999). They also have high weight specific metabolic rate and low fat reserves, making them vulnerable to desiccation and starvation. Due to these factors, immature ticks hatch in winter when temperatures are relatively low and the grass is tall, thus providing shelter. During this period, the grass is moribund with low nutritional content, thereby inducing low tick resistance to the host (Osofsky *et al.*, 2005). These factors increase survival capacity of immature ticks.

5.5 Influence of habitat and environmental factors on tick abundance at Imire Ranch

An increase in sward height resulted in increased tick abundance. However this factor was weakly correlated as the relationship was not linear. Huge tick loads were evidenced at medium sward height (60-80 cm), with lower tick loads in each extreme (Greenfield 2011). Drag sampling in tall grass misses some ticks as different developmental stages quest at different heights (Gallivan and Horak, 1997). Thus, the taller the grass, the greater is the variation in questing height among different tick stages. This results in some of the ticks being missed during drag sampling resulting in low tick density at high sward height (Greenfield, 2011). Ticks succumb to desiccation under short grasses (Horak *et al.*, 1983), explaining the low tick densities at low sward height.

No correlation was found between tick density and temperature, humidity, soil moisture and mat depth. High tick numbers were observed at temperatures between 21-30°C, which is in agreement with the review by Greenfield (2011). Temperatures falling above or below this range, however, resulted in reduced tick density. Under high temperature, ticks retreat beneath the mat to avoid desiccation, while under low temperature, questing activity is reduced until temperature reaches an optimal range (Randolph, 2004). Tick loads increased as

mat depth increased as observed by Greenfield (2011), but a mat depth greater than 40 mm was not associated with higher numbers.

High tick density was observed at low humidity (20-40%) which is collaborated by Greenfield (2011). However, very low humidity of 0-20% resulted in low tick density as supported by Estrada-Peña *et al.* (2013) as ticks failed to reabsorb moisture from the environment. However, at high humidity, ticks succumb to over saturation, thereby limiting their activity (Medlock *et al.*, 2008). Saturation deficit is thought to be correlated to tick survival and questing activity rather than relative humidity (Estrada-Peña and Salman, 2013). High tick abundances were observed at low soil moisture. This is supported by the study done by Greenfield (2011) in contrast to observations by Medlock *et al.* (2008) who recorded high tick abundance at high soil moisture. It therefore appears that tick questing behaviour is complex and is activated by a set of suitable conditions (Estrada-Peña *et al.*, 2013).

Tick questing activity can also be determined by other factors besides environmental factors, such as recruitment of newly moulted ticks or resumption of activity when favourable weather conditions commence (Estrada-Peña *et al.*, 2013). Other ticks may delay the onset of questing due to behavioural diapause, and older individuals may survive from previous questing periods and overlap with later moulted specimens, thereby confounding the correlation of tick activity with environmental factors (Estrada-Peña *et al.*, 2013). Management regime could also have influenced the results as some variation resulted from interaction of ticks with the control regime as suggested by Medlock *et al.* (2008).

Rhipicephalus larvae are known to favour sites with high sward height (De Garine-Wichatitsky *et al.*, 1999). They tend to avoid areas with short sward height even when the humidity is high as they have low energy reserves (Randolph and Storey, 1999) to allow them to descend regularly to replenish their body moisture. They also favour high soil moisture as it ensures that the air on the ground is moist enough to allow active uptake of moisture from

the air when they descend. Adult ticks, with their lower surface area to volume ratio, lower weight specific metabolic rate and higher energy reserve (Randolph and Storey, 1999), can venture into areas with short grasses. Hosts often overgraze preferred grasses, thus leaving them very short. Such grasses, however, possess high levels of host kairomones that make adult ticks akinetic (Carroll, 1998), thereby resulting in aggregation of ticks on such sites. In order to counteract the heavy desiccation experienced on such sites, high mat depth should be available to allow ticks to hide when weather conditions become unbearable. Questing then occurs when temperatures are low as a way of reducing moisture loss. This results in high adult populations in areas with short sward height, high mat depth and low temperature. As moisture re-absorption of ticks is dependent on relative humidity, the dominant tick species, *R. appendiculatus* and *R. evertsi*, exclude the less adapted species at sites with high humidity (see Ghosh and Tsutsui, 2012). This explains the frequency of *R. appendiculatus* and *R. evertsi* at sites with higher relative humidity and mat depth.

5.6 Sex ratio of ticks at Imire Ranch

The tick abundance of Males to females in the current study was not significantly different. Gender did not significantly change with season, habitat and sweeper type i.e. a change in habitat, sweeper type and season was not able to change this pattern. This conforms to observations made by Hornok and Farkas (2009) who characterised ixodid ticks by a 1:1 male to female ratio.

Minor variations in sex ratio which conform to changes in habitat type, sweeper type and season were, however, observed among questing *R. appendiculatus*. Females dominated across seasons and habitats. This observation collaborates earlier findings by Pinter *et al.* (2002). This is attributed to early questing and attachment of males to host so as to allow them to mate with several females (Hornok and Farkas, 2009). Males can attach to any host

irrespective of the presence of female ticks. Females, on the other hand, only attach when feeding males secrete attraction–aggregation–attachment (AAA) pheromones (Sonenshine, 2004). Thus, females will only attach to hosts infested by male ticks. This results in late attachment of female ticks. As the season progresses, less and less males remain questing as most will have already attached themselves to hosts and patiently waiting for females to mate. The cold-dry season had a higher female dominated sex ratio compared to the hot-wet season as many males are already attached to hosts.

5.7 Conclusion

The study revealed that cattle regularly treated with acaricides are an efficient means of controlling free-living ticks in cattle/wildlife mixed ranches. The efficacy of buffalo as a tick sweeper needs closer investigation as it did not have the same efficacy. Tick loads appeared to be influenced by season as tick developmental stages were heavily seasonal. Their abundance is also habitat dependent, which can be linked to host species preference and correlated to sward height.

Tick gender was not different with season, tick sweeper and habitat although a minor variation was observed on *R. appendiculatus*. As tick abundance and community composition and structure are heavily influenced by weather and host, an integrated tick control strategy is recommended for cattle/wildlife mixed ranges.

REFERENCES

- Allen, J.R. (1989). Immunology of interactions between ticks and laboratory animals. *Experimental & Applied Acarology*, **7**, 5–13.
- Ashford, R.W. (2001). *Encyclopedia of Arthropod-transmitted Infections of Man and Domesticated Animals* (New York: CABI).
- Barré, N. and Uilenberg, G. (2010). Spread of parasites transported with their hosts: case study of two species of cattle tick. *Revue Scientifique et Technique-Office international des épizooties*, **29**, 149–160.
- Bastos, A.D.S., Boshoff, C.I., Keet, D.F., Bengis, R.G. and Thomson, G.R. (2000). Natural transmission of foot-and-mouth disease virus between African buffalo (*Syncerus caffer*) and impala (*Aepyceros melampus*) in the Kruger National Park, South Africa. *Epidemiology & Infection*, **124**, 591–598.
- Bengis, R.G., Kock, R.A. and Fischer, J. (2002). Infectious animal diseases: the wildlife/livestock interface. *Revue Scientifique et Technique-Office International des Epizooties*, **21**, 53–66.
- Berkvens, D.L., Young, A.S. and Pegram, R.G. (1994). Collaborative research on behavioural diapause in adult *Rhipicephalus appendiculatus* populations. In tick and tick-borne disease control in east, central and southern africa, 1991-1994. *Proceedings of a joint OAU, FAO and ILRAD workshop*, Lilongwe, Malawi 25-28 April 1994 ILRI 1994.
- Biswas, S. (2003). Role of veterinarians in the care and management during harvest of skin in livestock species. *Proceedings National Seminar on Leather Industry in Today's perspective*. Kolkata, India.
- Carroll, J.F. (1998). Kairomonal activity of White-tailed deer metatarsal gland substances: A more sensitive behavioral bioassay using *Ixodes scapularis* (Acari: Ixodidae). *Journal of medical entomology*, **35**, 90–93.
- Carroll, J.F. (2003). How specific are host-produced kairomones to host-seeking ixodid ticks? In *Ticks and Tick-Borne Pathogens*, P.F. Jongejan, and P.W.R. Kaufman, eds. (Springer Netherlands), pp. 155–161.
- Chardonnet, P., Clers, B. des, Fischer, J., Gerhold, R., Jori, F. and Lamarque, F. (2002). The value of wildlife. *Revue Scientifique et Technique-Office international des épizooties*, **21**, 15–52.

- Condy, J.B., Hedger, R.S., Hamblin, C. and Barnett, I.T.R. (1985). The duration of the foot-and-mouth disease virus carrier state in African buffalo (i) in the individual animal and (ii) in a free-living herd. *Comparative Immunology, Microbiology and Infectious Diseases*, **8**, 259–265.
- Cumming, G.S. (1999). Host distributions do not limit the species ranges of most African ticks (Acari: Ixodida). *Bulletin of Entomological Research*, **89**, 303–327.
- Cumming, G.S. (2002). Comparing climate and vegetation as limiting factors for species ranges of African ticks. *Ecology*, **83**, 255–268.
- De Angelis, K.M. (2007). Measurement of soil moisture content by gravimetric method. *American Society of Agronomy*, 1–2.
- De Garine-Wichatitsky, M., De Meeûs, T., Guégan, J.-F. and Renaud, F. (1999). Spatial and temporal distributions of parasites: can wild and domestic ungulates avoid African tick larvae? *Parasitology*, **119**, 455–466.
- Diuk-Wasser, M.A., Gatewood, A.G., Cortinas, M.R., Yaremych-Hamer, S., Tsao, J., Kitron, U., Hickling, G., Brownstein, J.S., Walker, E., Piesman, J. and Fish, D. (2006). Spatiotemporal Patterns of Host-Seeking *Ixodes scapularis* Nymphs (Acari: Ixodidae) in the United States. *Journal of Medical Entomology*, **43**, 166–176.
- Dolan, T.T. (1992). Recent developments in the control of anaplasmosis, babesiosis and cowdriosis. *Proceedings Workshop held at ILRAD, 13 – 15 May 1991*. Nairobi Kenya
- Dugmore, H. (2012). Blazing or grazing – the great fire debate. *Farmers Weekly*.
[<http://www.farmersweekly.co.za/article.aspx?id=33151&>: Accessed 01 October 2015]
- Emmons, L.H. and Feer, F. (1997). *Neotropical rainforest mammals : a field guide*. University Press, Chicago.
- Estrada-Peña, A. (2001). Forecasting habitat suitability for ticks and prevention of tick-borne diseases. *Veterinary Parasitology*, **98**, 111–132.
- Estrada-Peña, A. and Salman, M. (2013). Current Limitations in the Control and Spread of Ticks that Affect Livestock: A Review. *Agriculture*, **3**, 221–235.
- Estrada-Peña, A., Gray, J.S., Kahl, O., Lane, R.S. and Nijhof, A.M. (2013). Research on the ecology of ticks and tick-borne pathogens—methodological principles and caveats. *Frontiers in Cellular and Infection Microbiology*, **3**(29), 1–12.
- Felix, D., Guerrero, A., Perez, D.L. and Andreotti, R. (2013). Acaricide research and development, resistance, and resistance monitoring. In: *Biology of Ticks*, D.E. Sonenshine, and R.M. Roe, (eds). Oxford University Press, New York.

- Fyumagwa, R.D., Runyoro, V., Horak, I.G. and Hoare, R. (2007). Ecology and control of ticks as disease vectors in wildlife of the Ngorongoro Crater, Tanzania : research article. *South African Journal of Wildlife Research*, **37**, 79–90.
- Gallivan, G.J. and Horak, I.G. (1997). Body size and habitat as determinants of tick infestations of wild ungulates in South Africa. *South African Journal of Wildlife Research*, **27**, 63–70.
- Ghosh, A. and Tsutsui, S. (2012). *Advances in Evolutionary Computing: Theory and Applications*. Springer Science & Business Media, New York.
- Gono, R.K., Chireshe, F., Muzondiwa, J.V. and Sichewo, P. (2014). Acaricide resistance in two tick species of veterinary importance in Zimbabwe. A case study of tick resistance to amitraz in the Mazowe District. *Midlands State University Journal of Science and Technology*, **5**(1), 111-120.
- Greenfield, B.P.J. (2011). Environmental parameters affecting tick (*Ixodes ricinus*) distribution during the summer season in Richmond Park, London. *Bioscience Horizons*, **4**, 140–148.
- Haddad, N.M., Holyoak, M., Mata, T.M., Davies, K.F., Melbourne, B.A. and Preston, K. (2008). Species' traits predict the effects of disturbance and productivity on diversity. *Ecology Letters*, **11**, 348–356.
- Horak, I.G. (1982). Parasites of domestic and wild animals in South Africa. XV. The seasonal prevalence of ectoparasites on impala and cattle in the Northern Transvaal. *Onderstepoort Journal of Veterinary Research*, **49**, 85–93.
- Horak, I.G. and Knight, M.M. (1986). A comparison of the tick burdens of wild animals in a nature reserve and on an adjacent farm where tick control is practised. *Journal of the South African Veterinary Association*, **57**, 199–203.
- Horak, I.G., De Vos, V. and Brown, M.R. (1983). Parasites of domestic and wild animals in South Africa. XVI. Helminth and arthropod parasites of blue and black wildebeest (*Connochaetes taurinus* and *Connochaetes gnou*). *Onderstepoort Journal of Veterinary Research*, **50**, 243–255.
- Hornok, S. and Farkas, R. (2009). Influence of biotope on the distribution and peak activity of questing ixodid ticks in Hungary. *Medical and Veterinary Entomology*, **23**, 41–46.
- Hove, T., Mukandi, R., Bere, M., Horak, I.G. and Latif, A.A. (2008). Ixodid ticks infesting domestic goats in communal land areas of Zimbabwe. *Journal of the South African Veterinary Association*, **79**, 116–120.

- Hubálek, Z. (2004). An annotated checklist of pathogenic microorganisms associated with migratory birds. *Journal of Wildlife Diseases*, **40**, 639–659.
- Jongejan, F., and Uilenberg, G. (1994). Ticks and control methods. *Revue Scientifique et Technique (International Office of Epizootics)*, **13**, 1201–1226.
- Jonsson, N. (2004). Integrated control programs for ticks on cattle: An: Examination of some possible components. *FAO animal production and health paper*. School of Veterinary Science, University of Queensland, Australia.
- Junquera, P. (2015). Spraying livestock against flies, ticks, mites, lice, mosquitoes, fleas and other external parasites of cattle, sheep, goats, pig and poultry. *Parasitipedia.net*. [http://parasitipedia.net/index.php?option=com_content&view=article&id=2425&Itemid=2690: Accessed 03 February 2016].
- Kahl, O. and Alidousti, I. (1997). Bodies of liquid water as a source of water gain for *Ixodes ricinus* ticks (Acari: Ixodidae). *Experimental & Applied Acarology*, **21**, 731–746.
- Keesing, F., Allan, B.F., Young, T.P. and Ostfeld, R.S. (2013). Effects of wildlife and cattle on tick abundance in central Kenya. *Ecological Applications*, **23**, 1410–1418.
- Kemp, D.H., Pearson, R.D., Gough, J.M. and Willadsen, P. (1989). Vaccination against *Boophilus microplus*: Localization of antigens on tick gut cells and their interaction with the host immune system. *Experimental & Applied Acarology*, **7**, 43–58.
- Kock, R.A. (2005). What is this infamous wildlife/livestock disease interface? A review of current knowledge for the African continent. *IUCN Species Survival Commission report on Conservation and Development Interventions at the Wildlife/Livestock Interface Implications for Wildlife, Livestock and Human Health*. S Osofsky (Ed). pp, 1-14.
- Latif, A.A., Hove, T., Kanhai, G.K., Masaka, S. and Pegram, R.G. (2001). Epidemiological observations of Zimbabwean theileriosis: Disease incidence and pathogenicity in susceptible cattle during *Rhipicephalus appendiculatus* nymphal and adult seasonal activity. *The Onderstepoort Journal of Veterinary Research*, **68(3)**, 187–195.
- Lindstrom, A. and Jaenson, T.G.T. (2003). Distribution of the Common Tick, *Ixodes ricinus* (Acari: Ixodidae), in Different Vegetation Types in Southern Sweden. *Journal of Medical Entomology*, **40(4)**, 375–378.
- Mapholi, N.O., Marufu, M.C., Maiwashe, A., Banga, C.B., Muchenje, V., MacNeil, M.D., Chimonyo, M. and Dzama, K. (2014). Towards a genomics approach to tick (Acari: Ixodidae) control in cattle: A review. *Ticks and Tick-borne Diseases*. **5(5)**, 475–483.

- Medlock, J.M., Pietzch, M.E., Rice, N.V.P., Jones, L., Kerrod, E., Avenell, D., Los, S., Ratcliffe, N., Leach, S. and Butt, T. (2008). Investigation of ecological and environmental determinants for the presence of questing *Ixodes ricinus* (Acari: Ixodidae) on Gower, South Wales. *Journal of Medical Entomology*, **45**, 314–325.
- Mekonnen, S., Bryson, N.R., Fourie, L.J., Peter, R.J., Spickett, A.M., Taylor, R.J., Strydom, T. and Horak, I.G. (2002). Acaricide resistance profiles of single- and multi-host ticks from communal and commercial farming areas in the Eastern Cape and North West Provinces of South Africa. *The Onderstepoort Journal of Veterinary Research*, **69**(2), 99–105.
- Mooring, M.S., Mazhowu, W. and Scott, C.A. (1994). The effect of rainfall on tick challenge at Kyle Recreational Park, Zimbabwe. *Experimental & Applied Acarology*, **18**, 507–580.
- Muhammad, G., Naureen, A., Firyal, S. and Saqib, M. (2008). Tick control strategies in dairy production medicine. *Pakistan Veterinary Journal*, **28**(1), 43–50.
- Mukhebi, A.W., Perry, B.D. and Kruska, R. (1992). Estimated economics of theileriosis control in Africa. *Preventive Veterinary Medicine*, **12**(1), 73–85.
- Nari, A. (1995). Strategies for the control of one-host ticks and relationship with tick-borne diseases in South America. *Veterinary Parasitology*, **57**(1), 153–165.
- Norval, R. A. I., Perry, B.D., Meltzer, M.I., Kruska, R.L. and Booth, T.H. (1994). Factors affecting the distributions of the ticks *Amblyomma hebraeum* and *A. variegatum* in Zimbabwe: implications of reduced acaricide usage. *Experimental & Applied Acarology*, **18**, 383–407.
- Nyahangare, E.T., Mvumi, B.M. and Stevenson, P.C. (2012). Tick control measures from nature. *Afgriland*, **56**(3), 76–77.
- Oliver, J.H. (1989). Biology and systematics of ticks (Acari: Ixodida). *Annual Review of Ecology and Systematics*, **20**, 397–430.
- Osofsky, S.A., Cleaveland, S., Karesh, W.B., Kock, M.D., Nyhus, P.J., Starr, L. and Yang, A. (2005). Conservation and Development Interventions at the Wildlife/livestock Interface: Implications for Wildlife, Livestock and Human Health : *Proceedings of the Southern and East African Experts Panel on Designing Successful Conservation and Development Interventions at the Wildlife/Livestock Interface : Implications for Wildlife, Livestock and Human Health, AHEAD (Animal Health for the Environment And Development) Forum, IUCN Vth World Parks Congress, Durban, South Africa, 14th and 15th September 2003*. Gland, Switzerland and Cambridge, UK.

- Perry, B.D., Mukhebi, A.W., Norval, R.A.I. and Barrett, J.C. (1990). *A Preliminary Assessment of Current and Alternative Tick and Tick-Borne Disease Control Strategies in Zimbabwe*. ILRI .
- Pinter, A., Labruna, M.B. and Faccini, J.L.H. (2002). The sex ratio of *Amblyomma cajennense* (Acari: Ixodidae) with notes on the male feeding period in the laboratory. *Veterinary Parasitology*, **105**, 79–88.
- Randolph, S.E. (2000). Ticks and tick-borne disease systems in space and from space. *Advances in Parasitology*, **47**, 217–243.
- Randolph, S.E. (2004). Tick ecology: processes and patterns behind the epidemiological risk posed by ixodid ticks as vectors. *Parasitology*, **129**, S37–S65.
- Randolph, S.E. and Storey, K. (1999). Impact of microclimate on immature tick-rodent host interactions (Acari: Ixodidae): implications for parasite transmission. *Journal of Medical Entomology*, **36**(6), 741–748.
- Ristic, I., Ambroise-Thomas, P. and Kreier, J.P. (2012). *Malaria and Babesiosis: Research findings and control measures*. Springer Science & Business Media, Netherlands.
- Schroder, B., Uys, A.C. and Reilly, B.K. (2006). A survey of free-living ixodid ticks on a commercial game farm in the Thabazimbi District, Limpopo Province, South Africa. *Journal of the South African Veterinary Association*, **77**, 141–144.
- Seifert, H.S.H. (1996). *Tropical Animal Health*. Kluwer Academic Publishers, London.
- Service, M. (2008). *Medical Entomology for Students*. Cambridge University Press, Edinburgh, U.K.
- Sonenshine, D.E. (2004). Pheromones and other semiochemicals of ticks and their use in tick control. *Parasitology*, **129**, S405–S425.
- Sonenshine, D.E. and Roe, R.M. (2014). *Biology of Ticks*. Oxford University Press, New York.
- Stachurski, F. (2006). Attachment kinetics of the adult tick *Amblyomma variegatum* to cattle. *Medical and Veterinary Entomology*, **20**(3), 317–324.
- Stewart, K. E. J., Bourn, N. A. D. and Thomas, J. A. (2001). An evaluation of three quick methods commonly used to assess sward height in ecology. *Journal of Applied Ecology*, **38**(5), 1148–1154.
- Sungirirai, M., Madder, M., Zandile, M., De Clercq, P. and Abatih, E.N. (2015). An update on the ecological distribution of the Ixodidae ticks in Zimbabwe. *Experimental and Applied Acarology*, **66**(2), 269–280.

- Sutherst, R.W., Maywald, G.F., Kerr, J.D. and Stegeman, D.A. (1983). The effect of cattle tick (*Boophilus microplus*) on the growth of *Bos indicus* × *B. taurus* steers. *Australian Journal of Agricultural Research*, **34**, 317–327.
- Swai, E.S., Karimuribo, E.D., Rugaimukamu, E.A. and Kambarage, D.M. (2006). Factors influencing the distribution of questing ticks and the prevalence estimation of *T. parva* infection in brown ear ticks in the Tanga region, Tanzania. *Journal of Vector Ecology*, **31**(2), 224–228.
- Tälleklint-Eisen, L. and Lane, R.S. (2000). Efficiency of Drag Sampling for Estimating Population Sizes of *Ixodes pacificus* (Acari: Ixodidae) Nymphs in Leaf Litter. *Journal of Medical Entomology*, **37**(3), 484–487.
- Terassini, F.A., Barbieri, F.S., Albuquerque, S., Szabó, M.P.J., Camargo, L.M.A. and Labruna, M.B. (2010). Comparison of two methods for collecting free-living ticks in the Amazonian forest. *Ticks and Tick-borne Diseases*, **1**(4), 194–196.
- Thomson, G.R. (1995). Overview of foot and mouth disease in southern Africa. *Revue scientifique et technique (International Office of Epizootics)*, **14**(3), 503–520.
- Tonnesen, M.H., Penzhorn, B.L., Bryson, N.R., Stoltz, W.H. and Masibigiri, T. (2004). Displacement of *Boophilus decoloratus* by *Boophilus microplus* in the Soutpansberg region, Limpopo Province, South Africa. *Experimental & Applied Acarology*, **32**(3), 199–208.
- Uilenberg, G. (2012). Veterinary significance of ticks and tick-borne diseases. In: *Tick Vector Biology: Medical and Veterinary Aspects*, B. Fivaz, T. Petney, and I. Horak (eds). Springer Science & Business Media, Berlin.
- Uys, A.C., Horak, I.G. and Harrison, A. (2015). Questing ixodid ticks on the vegetation of sable antelope and multi-herbivore enclosures in Thabazimbi. *Journal of the South African Veterinary Association*, **86**(1), 1–9.
- Walker, A.R., Bouattour, A., Camicas, J.-L., Estrada-Peña, A., Horak, I.G., Latif, A.A., Pegram, R.G. and Preston, P.M. (2003). *Ticks of domestic animals in Africa: a guide to identification of species*. Bioscience reports, Edinburgh.
- Walker, J.G., Klein, E.Y. and Levin, S.A. (2014). Disease at the wildlife-livestock interface: Acaricide use on domestic cattle does not prevent transmission of a tick-borne pathogen with multiple hosts. *Veterinary Parasitology*, **199**(3), 206–214.
- Western, D. (2013). Ecosystem conservation and rural development: the case of Amboseli. In: *Natural Connections: Perspectives In Community-Based Conservation*, M.R. Wright, and S.C. Strum (eds). Island Press, Washington, DC, USA, pp. 15–52.

- Willadsen, P. (1980). Immunity to Ticks. In: *Advances in Parasitology*, APL, W. H. R. Lumsden, R. Muller, and J. R. Baker (eds). Academic Press, London.
- Zieger, U., Horak, I.G., Cauldwell, A.E., Uys, A.C. and Bothma, J. du P. (1998). The effect of chemical tick control on cattle on free-living ixodid ticks and on tick parasitic on sympatric impala in the Central Province, Zambia. *South African Journal of Wildlife Research*, **28(1)**, 10–15.