

**FORAGING PREFERENCES FOR IMPALA (*Aepyceros melampus*) and
DIK-DIK (*Madoqua guntheri*) UNDER DIFFERENT LEVELS OF
PERCEIVED RISK IN A SAVANNAH ECOSYSTEM.**

By

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Declaration

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Dedication

To my girls: Angela, Neville and Lisa.

Abstract

Ecosystems are composed of heterogeneous landscapes characterized by different levels of forage availability, habitats and predation risk. Ewaso ecosystem in Laikipia, Kenya is such landscape and is composed of human-made glades within acacia bushland. Abundant and diverse community of large (> 5 kg) mammalian herbivores (LMH) and carnivores occur within this landscape. Whereas smaller-bodied LMH face greater predation and must forage on higher quality forage, larger-bodied LMH are more constrained by quantity rather than food quality or predation. Plants have anti-herbivory strategies such as chemical and mechanical defences. In response to risk and dietary limitations LMH exhibit a range of foraging behaviours in different habitats. This study was conducted between December 2012 and July 2014 at Mpala Research Centre and it looked into how predation risk coupled with plant defences, shape the foraging preference of impala and dik-dik using a modified giving up density (GUD) experiment with *A. brevispica*, *A. etbaica*, *Croton dichogamus* and *Grewia bicolor* as forage species. Random pairwise branch cuttings from the forage plants were placed in front of camera trap in the glades and the corresponding nearby bushlands. A total of 20 random sites and 10 trials per pairwise combination were used. Leaf biomass density was estimated before and after exposure to LMH. Foraging events from camera trap images and leaf biomass density remaining and removed were used to quantify forage preference and plant defence efficacy. Linear mixed effects models were used to test for the effect of habitat type on the forage preference and plant defence efficacy. Results show that impala were more selective in risky habitat and preferred the thorn-less *Grewia bicolor* and the less-mechanically defended *A. brevispica*. Dik-dik preferred the thorny and highly mechanically defended *A. etbaica* even in the risky habitats. Well defended plants, mechanically (e.g *A. etbaica*) or chemically (e.g *Croton dichogamus*), were safer from herbivory than less defended plants. For herbivores, risk of predation is more important than forage preference while for plants, defences are more important than habitat type. The study illustrated the important role pastoralists play in influencing the spatial variability in LMH diet choice and foraging behaviour within savannah ecosystem.

Keywords: Large Mammalian Herbivore (LMH), Predation Risk, Mechanical defences, Chemical defences, Giving Up Density (GUD), Foraging preference. Impala, Dik-dik.

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Abbreviations, Acronyms and Definitions

<i>A. brevispica</i>	<i>Acacia brevispica.</i>
<i>A. etbaica</i>	<i>Acacia etbaica.</i>
ANOVA	Analysis of variance.
C3	Carbon 3 forbs.
ca	Approximate
<i>Croton</i>	<i>Croton dichogamus</i>
Foraging events	Total number of images recorded by camera traps for impala and dik-dik foraging on each of the forage plants.
Glade	Open tree-less patches within <i>Acacia bushland</i> derived from abandoned livestock bomas.
<i>Grewia</i>	<i>Grewia bicolor</i>
GUD	Giving Up Density.
HSD	Honestly Significant Figures.
Larger-bodied LMH	LMH weighing about 50 kg (e.g impala)
LMH	Large Mammalian Herbivores. These are mammalian herbivores weighing from 5 kg and above.
LOF	Landscape Of Fear.
MRC	Mpala Research Centre.
MSc.	Master of Science.
Smaller-bodied LMH	LMH weighing about 5 kg (e.g dik-dik).
Spp.	Species.

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Chapter 1 : Introduction

1.1 Background

Terrestrial ecosystems are composed of patches that vary in food availability, habitat type, and predation risk (Brown *et al.*, 1979; McNaughton, 1979; Belovsky, 1981). This heterogeneity shapes the diversity and distribution of organisms (Druce *et al.*, 2009; Willems & Hill, 2009) because of the manner in which species partition different resources through their behaviour, movement patterns, and foraging preferences (Kartzinel *et al.*, 2015). Foraging theory posits that organisms will maximize energy intake while minimizing predation risk (Emlen, 1966; MacArthur & Pianka, 1966; Charnov, 1976; Brown, 1988, 1992). These models predict that a forager will stop depleting a patch when the benefits of harvest no longer exceed the sum of energetic, predation, and forgone opportunity costs of foraging (Brown & Mitchell, 1989; Brown, 1998, 1992; Makin *et al.*, 2012). For example, animals are predicted to spend more time foraging when predation risk is relatively low and when forage quality is relatively high (Moorcraft *et al.*, 2006). Thus, risk avoidance and energetic gain is a common trade-off faced by many organisms.

For ungulates, one of the key factors affecting predation risk is body size (Berger & Cunningham, 1988; Sinclair *et al.*, 2003; Radloff & du Toit, 2004). Smaller-bodied species are more vulnerable to predation (Sinclair *et al.*, 2003) and typically use cryptic anti-predator strategies, as opposed to larger species, which are more vulnerable to starvation and use early detection and evasion strategies to reduce risk (Jarman, 1974; Brashares *et al.*, 2000). These risk-forage trade-offs provide insight as to how diverse assemblages of Large (>5 kg) Mammalian Herbivores (LMH) coexist in East African savannahs (Ritchie & Olf, 1999).

While the risk of predation and resource abundance are commonly used gradients to assess forage-risk trade-offs in LMH, few studies have examined the role of plant defence. Plants have developed

several strategies to minimize loss of biomass to herbivores, such as chemical and mechanical (i.e. physical) defences like spines and thorns (du Toit, 2003; Borchard *et al.*, 2011). Plant defences either reduce the consumption rates or reduce the ability of herbivores to digest material once consumed (Belovsky *et al.*, 1991; Robbins, 1993).

Condensed tannins (a form of chemical defence) act as repellents to LMH by giving plants an undesirable, astringent taste (Harborne, 1991; Bryant *et al.*, 1992) or by reducing availability of protein and other nutrients (Robbins *et al.*, 1987) through protecting plant cell walls from being degraded in the rumen of LMH and inactivating digestive enzymes (Cooper & Owen-Smith, 1985). In other words, LMH can consume plants with high densities of tannins, but their ability to ferment and acquire nutrients from such material is inhibited.

Mechanical defences are thought to reduce intake rates of plant biomass (Cooper & Owen-Smith, 1986; Belovsky *et al.*, 1991; Gowda 1996), but have little effect on digestibility once consumed. Together, both mechanical and chemical defences limit resource availability for LMH and thus may serve as a key axis of niche differentiation among different-sized LMH.

Among LMH, larger-bodied (herein 40 – 50 kg: e.g impala) species are better able to digest coarse and more toxic plant material than smaller-bodied (5 - 10 kg: e.g dik-dik) species, which require higher densities of nutrients in their food but less total plant material (Underwood, 1982; Ritchie & Olff, 1999; Borchard *et al.*, 2011). Thus, chemical defences are likely more effective at deterring herbivory from smaller-bodied LMH species than larger-bodied ones. Many of the most apparent mechanical defences in African savannahs are thorns and spines on woody vegetation, especially those of the genus *Acacia*. Smaller-bodied LMH, such as dik-dik, have nimble mouthparts that enable them to manoeuvre around the spines and thorns of *Acacia*. Thus, mechanical defences are

probably better able to deter herbivory from larger-bodied LMH than smaller-bodied species. The very largest, or ‘mega-herbivores’ (e.g., elephants and giraffes), have generally escaped both predation and plant defences (Sinclair *et al.*, 2003).

Throughout savannahs in Laikipia, small patches of grass-dominated open areas (herein referred to as glades) of 0.2 – 1 ha occur within the acacia bushland and woodland communities (Young *et al.*, 1995; Augustine *et al.*, 2011). Glades are derived from abandoned livestock bomas, which are temporary livestock enclosures, and may persist for decades after they have been abandoned (Young *et al.*, 1995; Augustine, 2003). These glades contain nutrient enriched soil, and support a unique plant community dominated primarily by stoloniferous grass *Cynodon plectostachyus* (Young *et al.*, 1995; Augustine, 2003).

The glades are used by grazing and mixed-feeding LMH, likely to access the nutrient-rich grasses (Augustine, 2004) and or access to safety (Ford *et al.*, 2014) due to the increased visibility (Riginos & Grace, 2008). For example, glades are heavily used by impala in the dry season when grasses are dry and impala are foraging on bushes (Augustine, 2010; Augustine *et al.*, 2011). Many African LMH select for visibility because it enhances the detection and evasion of predators (Underwood, 1982; Hopcraft *et al.*, 2005; Riginos & Grace, 2008; Anderson *et al.*, 2010; Valeix *et al.*, 2011); however, this is not true for smaller-bodied LMH like dik-dik, who perceive open areas as risky (Jarman, 1974; but see Ford & Goheen, 2015). Recent work is pointing to the role of visibility in shaping the distribution and habitat utilization by larger-bodied LMH like the impala (Riginos & Grace, 2008; Ford *et al.*, 2014; Riginos, 2015). Visibility in glades is about double than that found in the surrounding bushland, just 100 m away from the glade edge (Ford *et al.*, 2014).

The purpose of this study, therefore, was to use an experimental approach to determine the extent to which risk of predation, plant defence, and LMH body size interact to shape foraging behaviour and the impact of herbivory on trees, via two sympatric browsers: the 5 kg dik-dik and the 50 kg impala.

1.2 Rationale for the Study

With the growing utilization of domestic browsers (camels, goats) for human livelihoods, understanding the foraging preferences of wild browsers is essential for the stewardship of natural landscapes. Decades of developing the science and cultural practices of coexistence between livestock and wildlife have largely focused on cattle-grazer interactions (Odadi *et al.*, 2011a; Odadi *et al.*, 2011b; Augustine, 2003). However, throughout Laikipia County, Kenya, foraging preferences by browsers is largely unknown, despite browsers making up the majority of wildlife in this area (O'Brien & Kinnaird, 2011). Because wild browsers can affect the abundance and distribution of forage (Ford *et al.*, 2014), it is important that we better understand how risk of predation changes the forage preference of wildlife. This information would be critical to developing sound land management practices that ensure the coexistence of wildlife populations and human livelihoods.

In addition to shifting range management practices, ecosystems in many areas may transform under climate change (Sala *et al.*, 2000). Climate change is predicted to have major adverse effects in arid and semi-arid landscapes, such as Laikipia, with increases in shrub encroachment (i.e. the increase in woody plant cover) into formerly open and grassy areas (Archer *et al.*, 1995; Jörg & Jeltsch, 2004). Shrub encroachment has adverse effects on the cattle carrying capacity (Jeltsch *et al.*, 1997; Roques *et al.*, 2001) and biodiversity (Meik *et al.*, 2002). Given that impala avoid bushy areas to lower the risk of predation (Underwood, 1982; Estes *et al.*, 1999; Hopcraft *et al.*, 2005;

Riginos & Grace, 2008; Anderson *et al.*, 2010; Valeix *et al.*, 2011; Ford *et al.*, 2014), and dik-dik avoid open areas (Jarman, 1974; Ford & Goheen, 2015), bush encroachment is likely to affect the diet selection and foraging behaviour of these LMH. In order to develop sound management practices, it is therefore paramount to understand what forage species these LMH feed on and where, in terms of predation risk.

1.3 Problem Statement

Although the link between predation risk and habitat use by terrestrial LMH has been well established (Lima & Dill, 1990; Lima 1998; Brown *et al.*, 1999; Laundré *et al.*, 2001; Verdolin 2006; Ford *et al.*, 2014; Ford & Goheen, 2015), there is paucity (if not lacking altogether) of studies that have focused solely into how plant defences (mechanical or chemical) interplay with predation risk in influencing foraging behaviour of sympatric LMH with varying body size and in habitats varying in levels of predation risk. This study used a modified GUD to determine the extent to which plant defences interact with predation risk to influence the foraging behaviour of impala and dik-dik in a heterogeneous savannah landscape.

1.4 Main Objective

The objective of this study was to determine the foraging preference of two LMH species under different levels of perceived risk. The focus was on impala *Aepyceros melampus* (ca. 50 kg), and Guenther's dik-dik *Madoqua guentheri*, (ca. 5 kg), and their consumption of four species of trees: *Acacia brevispica*, *A. etbaica*, *Grewia spp* and *Croton dichogamus*. These tree species are the most abundant at Mpala Research Centre (Young *et al.*, 1995) and exhibit different levels of plant defences against herbivory.

1.4.1 Specific Objectives

The following were the specific objectives of the study.

1. To determine if forage preference for impala and dik-dik changes with habitat types varying in predation risk.
2. To determine if impala and dik-dik prefer the same forage species.
3. To determine if forage preferences are driven by plant defences.
4. To determine the efficacy of plant defences against herbivory by impala and dik-dik.

1.5 Study Hypotheses

Under this study the following hypotheses were tested:

A.) Palatability-Driven Foraging: Plant defences drive foraging preferences for both LMH equally, such that the preferred forage species would be the same for both LMH irrespective of body size or level of risk. The prediction was that *Grewia bicolor* and *A. brevispica* would be preferred to *A. etbaica* and *Croton dichogamus*. *A. etbaica* is highly mechanically defended (presence of long and short thorns) whereas *Croton dichogamus* is highly chemically defended (high tannin content) (Hemayet *et al.*, 2012).

B.) Accessibility-Driven Foraging: Mechanical plant defences drive foraging preferences for both LMH, such that the preferred forage would be the most poorly-defended mechanically irrespective of LMH identity. Because *A. etbaica* is better defended mechanically (with both long spines and short curved spines) than *A. brevispica* (with only short less curved spines), whereas *Grewia bicolor* and *Croton dichogamus* do not have any thorns or spines to deter accessibility, it was predicted that *A. etbaica* would be least preferred by both LMH.

C.) Risk-Sensitive Foraging: The preferred forage species would depend on whether the LMH encounters the plant in a safe or risky area. In safe areas, LMH would prefer mechanically defended plants because they can afford to spend the time required to access leaves among spiny defences. In risky areas, LMH would prefer chemically defended plants because they are trading off acquisition time (intake) with handling time (digestion). In this case, digestion may occur while engaging in more vigilant behaviour or in a safer habitat. The prediction was that in high risk areas the LMH would prefer the thorn-less *Croton dichogamus* and *Grewia bicolor* while in low risk areas they would prefer the thorny *A. etbaica* and *A. brevispica*.

However, differences in allometric scaling of gut capacities, metabolic rate, and predation rates modified the above hypotheses in the following manner:

I.) Palatability-Driven Foraging: With faster rates of digestion, larger-bodied LMH can more easily overcome chemical defences, require greater intake per day, and are less selective than smaller-bodied LMH. Therefore, the effect of plant defence on foraging preference should be stronger for smaller-bodied LMH species than larger-bodied ones. It was predicted that the magnitude of selection for *Grewia bicolor* and *A. brevispica* relative to *A. etbaica* and *Croton dichogamus* would be greater for dik-dik than impala.

II.) Accessibility-Driven Foraging: With their smaller mouthparts, smaller-bodied LMH are better equipped to avoid mechanical defence than larger-bodied LMH. Therefore, preference for plants with different amounts of mechanical defence should be greater for larger-bodied species. Under this hypothesis, it was predicted that the magnitude of selection for *A. brevispica* over *A. etbaica* would be greater for impala than dik-dik.

III.) Risk-Sensitive Foraging: Smaller-bodied LMH experience more risk than larger ones, and tend to use denser vegetation under riskier conditions. Larger-bodied LMH tend to use open areas to minimize risk. Here, it was predicted that dik-dik would spend more time foraging in bush and impala would spend more time foraging in open areas. Likewise, dik-dik would be more selective than impala in open areas where they perceive greater risk and require more return per unit time. Conversely, impala would be more selective than dik-dik in bushy areas where they perceive greater risk.

Chapter 2 : Literature Review

2.1 Ewaso Ecosystem

Georgiadis (2011) defined Ewaso ecosystem by the geographical extents of two large-scale processes; the dry-season river flow and the elephant migration. Two major water-towers, the Aberdare Range and Mt. Kenya, collect much of the regions' rainfall and are drained mainly by two permanent rivers: the Ewaso Nyiro and Ewaso Narok, which flow into the Lorian Swamp (Georgiadis, 2011). The functional ecosystem "boundary" of Ewaso ecosystem encompasses the upper drainage basin of the Ewaso Nyiro and Ewaso Narok rivers and covers about 40,000 km² within Laikipia County and parts of adjacent Samburu, Meru, Isiolo, and Marsabit Counties (Georgiadis, 2011). There is abundant wildlife in this region and they mostly occur in the southwestern section of the region, on private ranches in Laikipia County (Georgiadis, 2011).

Ewaso ecosystem is a human-wildlife occupied landscape with abundant native ungulate populations occurring on rangelands outside formally protected areas alongside livestock (Georgiadis, 2011). Wildlife in this system share most of the landscape with varying densities of people and livestock and only about 6% of the total land area has protection status (Georgiadis, 2011). This livestock-wildlife co-existence is very critical for the conservation of wildlife in this region (Prins *et al.*, 2000). Previous studies have shown that these interactions are important to both the livestock and wild ungulates and can either be negative (competition) or positive (facilitation) (Augustine *et al.*, 2011; Odadi *et al.*, 2011a; Prins *et al.*, 2000).

2.2 Formation of Glades and Landscape Heterogeneity

Predators, apart from influencing the behaviour of LMH (Laundre *et al.*, 2001), can also indirectly influence the pastoralist's livestock husbandry practices (Augustine, 2003; Augustine, 2004). The

presence of complete assemblage of carnivore species within Ewaso ecosystem landscape (O'Brien & Kinnaird, 2011; Woodroffe, 2011), over the centuries has warranted the need for the pastoralists to find ways of protecting their livestock from depredation and one such way is through corralling their livestock at night in bomas made from thorny *Acacia* trees. These bomas are temporary structures which are usually abandoned when the pastoralists relocate to new locations in search of greener pastures (Young *et al.*, 1995; Augustine, 2003). The bomas are traditionally made by clearing bushland and using thorny *Acacia* trees as fence to keep off the predators. Over time, this husbandry practice has led to proliferation of small patches of tree-less, grass-dominated open areas of 0.2 – 1 ha occurring within the *Acacia* bushland and these are generally referred to as glades (Young *et al.*, 1995; Augustine *et al.*, 2011). These glades contain nutrient enriched soil, and support a unique plant community dominated primarily by the stoloniferous grass *Cynodon plectostachyus* (Young *et al.*, 1995; Augustine 2003). Within Mpala Research Centre (MRC) these glades occur at a density of between 0.71 km⁻² and of 1.21 km⁻² for over decades and none has ever reverted to bushland (Augustine, 2003).

These glades form a mosaic of open patches within the *Acacia* bushland providing a heterogeneous landscape. Landscape heterogeneity, in terms of vegetation distribution and predation risk, can significantly influence the local distribution and abundance, and the foraging behaviour of wild herbivores (Young *et al.*, 1995; Laundre *et al.*, 2001; Seargent *et al.*, 2007; Riginos & Grace, 2008; Ford *et al.*, 2014; Ford & Goheen, 2015). In terrestrial savannah ecosystems, variation in LMH body size and the dietary tolerance, has been shown to results in varying diet and habitat selectivity across LMH species (du Toit & Owen-Smith, 1989). This together with the functional differences between grazing and browsing guilds (Prins & Douglas-Hamilton, 1990; Fritz *et al.*, 2002) contributes to the high heterogeneity of the landscapes in this ecosystem (du Toit, 2003).

2.3 Optimal Foraging Theories

LMH, due to the predation risk posed by the presence of carnivores are known to exist in a ‘‘Landscape of Fear’’ (LOF) (Laundre *et al.*, 2001; Brown & Kotler, 2004) and they must often trade-off between avoiding predators and maximizing the quality and or quantity of their forage intake (Sih, 1980; Lima, 1998; Houston *et al.*, 1993). The nature of this trade-off is dependent on herbivores’ perceived degree of predation risk (Brown & Kotler, 2004).

Foraging theories (Emlen, 1966; MacArthur & Pianka, 1966; Charnov, 1976; Brown, 1988, 1992) posits that LMH will always seek to maximize energy intake while minimizing predation risk and are predicted to match their resources when predation risk is low and to trade off food for safety by avoiding dangerous habitats when risk is high (Power, 1984a, 1984b; Abrahams & Dill, 1989; van Baalen & Sabelis, 1993). These models predict that animals will spend more time foraging in a given habitat when the predation risk is lower and when forage quality is high and will spend less time foraging when predation risk is high and forage quality is low (Moorcraft, *et al.*, 2006). They do so by either reducing the time spent foraging and or increasing their level of vigilance while foraging in riskier habitats (Sih, 1980; Lima & Dill, 1990; Kotler *et al.*, 1994; Brown, *et al.* 1999). LMH rely heavily on behavioural responses (e.g vigilance) to nonlethal predation risk (Brown *et al.*, 1999) and various studies have supported this for a variety of LMH species (Underwood, 1982; Lagory, 1986; Scheel, 1993; Bednekoff & Ritter, 1994; Molvar & Bowyer, 1994; Ford & Goheen, 2015).

2.4 Predation Risk and Foraging Behaviour

LOF is as a result of the risk of predation and it is the way in which prey perceive differing habitats having differing levels of predation risk within a landscape (Laundre *et al.*, 2001). It quantifies how LMH avoid predation risks in space (Laundre *et al.*, 2001) and has been used to understand

how animals behave in terrestrial (Brown *et al.*, 1999; Kotler *et al.*, 2002; Brown & Kotler, 2004, Ford & Goheen, 2015) and marine ecosystems (Wirsing *et al.*, 2008). In such a landscape, LMH must often trade-off between avoiding predators and maximizing the quality and or quantity of their forage intake (Sih, 1980; Houston *et al.*, 1993; Lima, 1998).

Predation risk has been known to do directly or indirectly affect physiology (Sheriff *et al.*, 2009) and behaviour of animals (Lima & Dill, 1990; Ford *et al.*, 2014; Ford & Goheen, 2015). This implies that animals adjust their use of space to their perception of the distribution of predation risk (Lima & Dill, 1990; Brown & Kotler, 2004; Cresswell, 2008). It is important to note that LOF for different LMH species is never uniform and one of the key factors affecting predation risk in LMH is the body size (Berger & Cunningham, 1988; Sinclair *et al.*, 2003; Radloff & du Toit, 2004). Smaller-bodied LHM species are more vulnerable to predation (Sinclair *et al.*, 2003) and typically use cryptic anti-predator strategies, as opposed to larger-bodied LMH species, which are more vulnerable to starvation and use early detection and evasion strategies to reduce risk (Jarman 1974; Brashares *et al.*, 2000). These risk-forage trade-offs provide insight as to how diverse assemblages of LMH coexist in East African savannahs (Ritchie & Olf, 1999).

Carnivores predating on herbivorous animals can have a cascading effect on plant populations by either altering herbivore density through direct consumption, or indirectly through mediating prey forage behaviour, or both (Rosenzweig, 1973; Oksanen *et al.*, 1981; Abrams, 1996). The presence of predators in itself represents a risk of predation to herbivores that can mediate predator–plant interactions by altering herbivore prey foraging behaviour (Abrams, 1996; Ford *et al.*, 2004; Ford & Goheen, 2015) and this can lead to marked changes in plant biomass, distribution, and diversity (Crawley, 1983). Thus, predators affect plants indirectly by altering spatial patterns of LMH herbivory (Abrams 1995; Schmitz 2003, Schmitz *et al.*, 2004, Ford *et al.*, 2014).

2.5 Role of Plant Defences in Foraging Preference

Plants over centuries of evolution have developed several counter measure strategies to minimize loss of plant material to LMH. These strategies include mechanical (i.e physical) defence such as thorns and spines (Myers & Bazeley, 1991), chemical defence e.g tannin content (McNaughton & Tarrants, 1983; du Toit *et al.*, 1990; Bryant *et al.*, 1992; Ward *et al.*, 1997), growth strategies (for instance, growing too tall for the leaves to be eaten, Milewski *et al.*, 1991; Palo *et al.*, 1993), and low nutrient content (Lundberg & Astrom, 1990). Plant defences act by either reducing the consumption rates or by reducing the ability of herbivores to digest material once ingested (Belovsky *et al.*, 1991; Robbins, 1993).

Mechanical defences, generally act by reducing the rates at which plant materials can be ingested by herbivores (Belovsky & Schmitz, 1994; Cooper & Owen-Smith, 1986; Belovsky *et al.*, 1991; Gowda, 1996). Thorns and spines require herbivores to manoeuvre before harvesting so that the thorns or spines do not "prick" the forager (Belovsky & Schmitz, 1994) thus mechanical defences modify the feeding-time constraint and therefore thorny plants should take longer, on average, to harvest than the thorn-less plants (Cooper & Owen-Smith, 1986). The condition required for the thorns to be an effective mechanical defence is that the nutrient content per unit of digestive constraint utilized must be greater for the defended plant (Belovsky & Schmitz, 1994). However, mechanical defences cannot be attributed with universal efficacy, rather, efficacy depends upon the context of body mass of LMH and the attributes of other plants available to the herbivore in the immediate environment (Belovsky & Schmitz, 1994).

Condensed tannins, as a form of chemical defence, on the other hand, act as repellents to LMH by giving plants an undesirable, astringent taste (Harborne, 1991; Bryant *et al.*, 1992) or by reducing

availability of protein and other nutrients (Robbins *et al.*, 1987) through protecting plant cell walls from being degraded in the rumen of LMH and inactivating digestive enzymes (Cooper & Owen-Smith, 1985). For any plant chemical to be a successful defence it must attain a threshold of digestion-inhibition before it reduces consumption and any further ability to reduce digestion does not reduce consumption any further (Belovsky & Schmitz, 1994). However, the effects of the chemical are not always so apparent and higher quantity of the chemical does not always lead to reduced consumption (Belovsky & Schmitz, 1994).

The effect of tannin as a chemical defence is dependent on the type of tannin consumed, its chemical structure and molecular weight, the amount ingested, and the animal species involved (Behmer *et al.*, 2002; Frutos *et al.*, 2004). High concentrations of tannins reduce voluntary feed intake and nutrient digestibility, whereas low to moderate concentrations may improve the digestive utilisation of feed mainly due to a reduction in protein degradation in the rumen and a subsequent increase in amino acid flow to the small intestine (Barry *et al.*, 1986; Frutos *et al.*, 2004).

Investing in defences are costly for plants and come at the expense of growth and reproduction (Briggs & Schultz, 1990; Palo *et al.*, 1993). Due to the costs of defence, plants investing in mechanical defences have been associated with low densities of chemical defences (Moles *et al.*, 2013; Ward & Young, 2002).

Larger-bodied LMH species, like impala, are known to require higher densities of nutrients in their food but less total plant material and due to their large gut capacity are able to digest coarse and more toxic plant materials (Underwood, 1982; Ritchie & Olf 1999; Borchard *et al.*, 2011). Smaller-bodied LMH (e.g dik-dik), on the other hand, with their nimble mouth parts are able to

navigate around the thorns more effectively than the impalas and thus chemical defences are likely more effective at deterring herbivory from smaller-bodied LMH species than larger-bodied species. The very largest, or ‘mega-herbivores’ (e.g., elephants and giraffes), have generally escaped both predation and plant defences (Sinclair *et al.*, 2003). Together, both mechanical and chemical defences limit resource availability for LMH and thus may serve as a key axis of niche differentiation among different-sized LMH.

2.6 Gaps in Predation Risk Mediated Foraging Behaviour Studies

Several studies have described the effects of habitat types and predation risk on foraging behaviour for a number of taxa including deer *Odocoileus* spp (Altendorf *et al.*, 2001; Lingle, 2002), caribou *Rangifer tarandus* (Whittington *et al.*, 2011), guanaco *Lama guanicoe* (Marino & Baldi, 2008), antelope (Jarman, 1974; Underwood, 1982; Sinclair & Arcese, 1995; Valeix *et al.*, 2009; Ford *et al.*, 2014), elk (Fortin *et al.*, 2005; Kuijper *et al.*, 2013), Nubian ibex *Capra nubiana* (Iribaren & Kotler, 2012), and moose *Alces alce* (Berger, 2007; Gervasi *et al.*, 2013). Though there are a few studies that have focussed on the role of predation risk in mediating behavioural change in smaller-bodied LMH like dik-dik (e.g Ford & Goheen, 2015), most have solely focused on larger (> 40 kg) and gregarious species that typically alter group size in response to predation risk (Dehn, 1990; Fortin & Fortin, 2009; Taraborelli *et al.*, 2014), avoid risky areas (Kuijper *et al.*, 2013; Ford *et al.*, 2014), and often increase use of open habitats to facilitate detection of predators (Anderson *et al.*, 2010; Ford *et al.*, 2014). This emphasis on larger-bodied LMH species does not represent the diversity of life-history traits among LMH.

From the available body of work, it has also emerged that the response of herbivores to predation risk is not homogenous across LMH but is rather specific to species (Ford & Goheen, 2015). Sympatric species of prey may respond to risk in different ways, even when hunted by the same

predator species (Lingle, 2002; Periquet *et al.*, 2012; Gervasi *et al.*, 2013). This would therefore mean that LMH functional traits such as body size, sociality, feeding style, would influence how different LMH behave in habitats varying in predation risk (Ford & Goheen, 2015). Due to this species specific response to predation risk, several studies on different LMH species with varying traits across different systems are needed (Ford & Goheen, 2015) before a predictive theory can be fully developed (Creel, 2011).

While the link between predation risk and habitat use by terrestrial herbivores has been well established (Lima & Dill, 1990; Lima 1998; Brown *et al.*, 1999; Laundré *et al.*, 2001; Verdolin, 2006), there is no much studies presently known that have looked into how plant defences (mechanical or chemical) interplay with predation risk in influencing foraging behaviour of sympatric LMH with varying body size.

Chapter 3 : Methodology

3.1 Study Area

The study was conducted between December 2012 and July 2014 at Mpala Research Centre (MRC) in Laikipia County, Kenya (0° 17' N, 37° 53' E) at 1600 - 1800 m above sea level (Figure 3.1). The research centre and the associated Mpala Ranch comprises ca. 190 km² of semi-arid savannah where people, livestock and wildlife coexist, thereby offering opportunity to use ecological insights to inform land management (Odadi *et al.*, 2011a; Ford *et al.*, 2014). Rainfall averages 508 mm per annum and is weakly trimodal, with a major peak in April-May, and minor peak in August, and October-November (Augustine, 2010).

Two major soil types underlie MRC. Poorly-drained volcanic vertisols (i.e., 'black-cotton' soil) underlie ca. 10% of MRC, and support a plant community dominated by the tree *Acacia drepanolobium* and a continuous understory that includes the grasses, *Agrostis spp*, *Lintonia nutans*, and *Themada triandra*, and the forbs *Aerva lanata*, *Commelina spp*, *Dyschoriste radicans*, *Indigofera spp.* and *Rhinacanthis ndorensis* (Young *et al.*, 1995; Young *et al.*, 1998). The remaining red, sandy loam soils exhibit a higher diversity of woody species, including *Acacia brevispica*, *A. etbaica*, *A. mellifera*, *Croton dichogamus* and *Grewia bicolor* with a discontinuous understory dominated by the grasses *Cynodon dactylon*, *Digitaria milanjana*, *Pennisetum mezianum*, and *P. stramineum* (Augustine & McNaughton, 2004).

Across MRC, abandoned livestock corrals ('bomas') persist as treeless, nutrient-rich lawns ('glades') that are embedded within a background of *Acacia*-dominated bushland (99% of the landscape) (Young *et al.*, 1995).

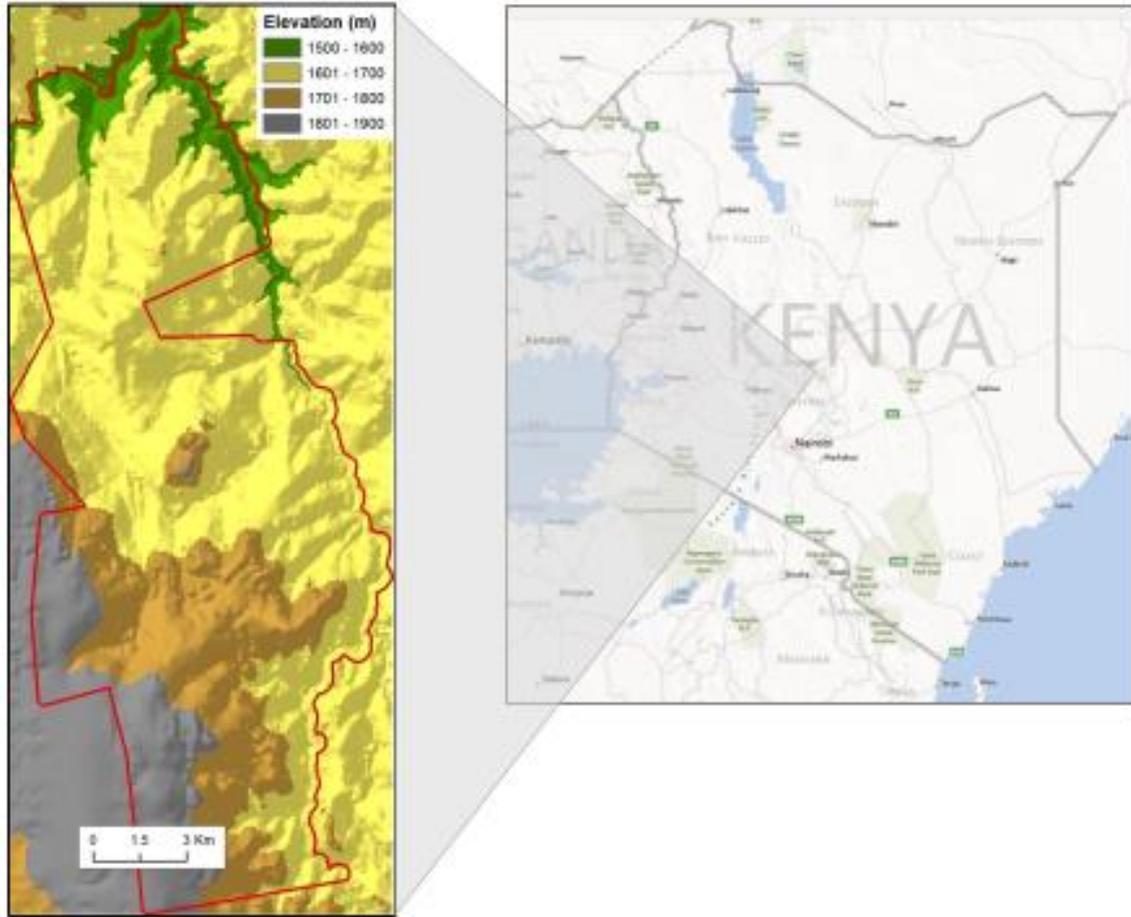


Figure 3.1 Map of Mpala Research Centre and associated Mpala conservancy.

The native herbivore biomass density at MRC stands at ca. 5,282 kg per km² of which the most abundant are elephant (*Loxodonta africana*) at 2,882 kg per km², impala (*Aepyceros melampus*) at 813 kg per km², and dik-dik (*Madoqua guentheri*) at 693 kg per km² - making over 80% of the total wild herbivores biomass at the study area (Augustine, 2010). Other herbivores found in this area include: zebra (*Equus burchellii*), giraffe (*Giraffa camelopardalis*), waterbuck (*Kobus ellipsiprymnus*), buffalo (*Syncerus caffer*), eland (*Taurotragus oryx*), and scrub hares (*Lepus saxatilis*) (Augustine, 2010).

Native large (> 20 kg) predators occurring in this area include African wild dog (*Lycaon pictus*), lion (*Panthera leo*), leopard (*P. pardus*), spotted hyena (*Crocuta crocuta*), and striped hyena

(*Hyaena hyaena*) (Woodroffe, 2011; Ford *et al.*, 2014; Ford & Goheen, 2015). They occur at a combined density of ca. 35 individuals per 100 km² (Ford *et al.*, 2014).

3.2 Study Species

3.2.1 Impala *Aepyceros melampus* (Lichtenstein, 1812)

Impala are a medium-sized African antelope, ranging between 75 and 95 cm at the shoulder and weighing between 40 and 60 kg (Plate 3.1a). Impala are water-dependent and occur along ecotones associated with light woodlands and savannahs in Kenya, Tanzania, Swaziland, Mozambique, northern Namibia, Botswana, Zambia, Zimbabwe, southern Angola, north-eastern South Africa, and Uganda. Impala are almost wholly grazers during the rains and during the dry season they are mostly in the woodlands, browsing on shrubs, herbs, pods, and seeds (Kingdon, 1997). They are the most dominant ungulate (over 50% of biomass) among the MRC resident herbivores and occur at biomass densities of 813 kg per km² (Augustine, 2002).

3.2.2 Guenther's dik-dik *Madoqua guntheri* (Günther, 1894)

Dik-dik (Plate 3.1b) are a small monogamous and territorial antelope in the genus *Madoqua* that live in the bushland of eastern and southern Africa and are specialized in feeding on C3 (non-grass plants) forbs and trees (Kingdon, 1997; Cerling *et al.*, 2003; Manser & Brotherton, 1995). They stand at about 30–40 cm at the shoulder, are 50–70 cm long, weigh 3–6 kg and can live for up to 10 years (Kingdon, 1997). Dik-dik are numerous at MRC. They are the third most abundant after elephant and impala and occur at density of 693 kg per km² (Augustine, 2010).



(a)



(b)

Plate 3.1 Focal herbivore species in this study. (a) Impala *Aepyceros melampus* and (b) Dikdik *Madoqua guntheri*.

3.2.3 Forage Species

Forage plant species in this study were; *Acacia brevispica*, *A. etbaica*, *Croton dichogamus* and *Grewia bicolor*. They make up more than 80% of woody stems at the study site (Ward & Young, 2002; Young *et al.*, 1995) and exhibit a range of defence traits (Plate 3.2). *A. brevispica* is characterized by small thorns, and large leaves. Although there were no data on chemical bioassays of all plant defence compounds for these four species, data from herbivore enclosure experiments suggests that differences in chemical defences among *A. etbaica* and *A. brevispica* are irrelevant for impala foraging (Ford *et al.*, 2014), that *A. etbaica* is the best mechanically-defended species of these four plants (Ford *et al.*, 2014), and that *Croton dichogamus* is most likely the best defended chemically (Young *et al.*, 1998). *Grewia bicolor* and *Croton dichogamus* has no spines or thorns but *Croton* spp. has been recorded elsewhere to have higher tannin content (Hemayet *et al.*, 2012; Table 3.1). Tannin content for various species of *Grewia* and *Croton* from other studies are included in Table 3.1.

Table 3.1 Tannin content for *Grewia* and *Croton* species.

Forage Species	Total Extractable tannin	Total Condensed Tannin	Total Tannin Content	Source
<i>Grewia carpinifolia</i>	1.78 ± 0.024 ^a	0.89 ± 0.01 ^a	-	Apori <i>et al.</i> , 1998
<i>Croton sporsiflorus</i>	-	-	257.31 ± 0.82 ^b	Hemayet <i>et al.</i> , 2012
<i>Acacia brevispica</i>	32 ± 46.5 ^c	1.1 ± 3.2 ^d	-	Abdulrazaak <i>et al.</i> , 2000

^a % DM ± Standard error of the difference (SED).

^b mg of tannic acid equivalent per gm of dry extract. ± Standard Error of Mean (SEM).

^c mg/g DM ± Standard Error of Mean (SEM).

^d mg/g DM ± Standard Error of Mean (SEM).

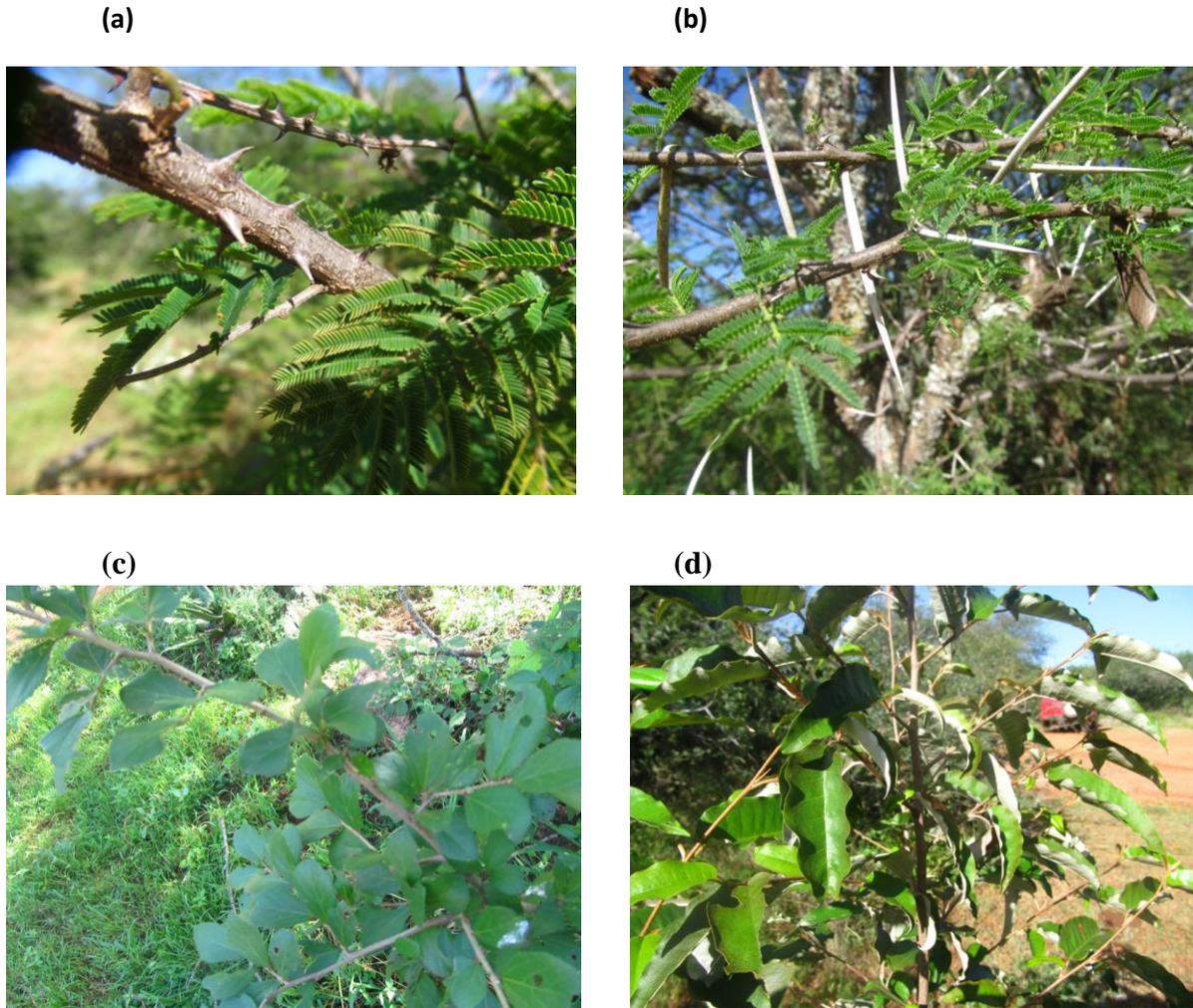


Plate 3.2 Focal forage species. (a) *Acacia brevispica*, (b) *A. etbaica*, (c) *Grewia bicolor* and (d) *Croton dichogamus*.

3.3 Field Experiment Setup

A modified approach to giving-up density (GUD) technique was employed to test the hypotheses. GUD is the density of food remaining in a patch after a forager has stopped utilizing the patch (Brown, 1988). GUD was developed to quantify different aspects of foraging behaviour in a natural setting, such as perceived food availability and predation risk (Brown, 1988, 1992). Specifically, the following were recorded;

- 1) The foraging events of impala and dik-dik for the four species of trees;

- 2) The number of leaves remaining after visitations by impala and dik-dik; and
- 3) The number of leaves removed after exposure to herbivores was also calculated.

Forage tree species of focus were *Acacia brevispica*, *A. etbaica*, *Croton dichogamus* and *Grewia bicolor* which make up >80% of stems at MRC (Ward & Young, 2002; Young *et al.*, 1995) and exhibit a range of mechanical and chemical defences.

Branch cuttings (ca. 150 cm tall) from random pairwise combination of forage species were placed ca. 8 m in front of motion sensitive camera trap (Plate 3.3). The pair-wise branch cuttings were set at 1 m apart and were anchored in pots filled with soil and water to maximize longevity of green foliage. Pots were dug into the ground with their tops level with the ground and covered with local substrate to minimize animals' perceptions of human activity. The random pairwise combinations were placed in three plots per study site, one in the centre of the glade and two in the surrounding bushland, about 50 m from the edge of the glades, to increase probability of encounter in the bushland sites. The plots in the bushland were set in areas with signs of focal species (e.g., game trails, dung middens) to maximize probability of encounter. Leaves were counted around mid-day after two days. Of all the glades available within the study site, a total of 20 were used for this study. These were randomly selected but only glades that showed signs (e.g fresh droppings, game trails) of recent use by impala and dik-dik were used. Only one of the glades that were likely to be used by same group of impalas, based on GPS telemetry (Ford *et al.*, 2014), were used for the experiment. Of the four tree species used in this study, there were a total of six pairwise combinations. Ten trials were setup for each of the six pairwise combination giving a total of 600 trials.

Motion sensitive camera traps of Reconyx RM45 model (RECONYX, Inc., Holman, WI, USA) were used. They were set to take 5 pictures per trigger with no delay between trigger intervals. In order to minimize biases brought about the angle of field of view and detection zone (Trollet *et al.*, 2014) camera traps of the same make and model were used throughout the experiment.



Plate 3.3 Photos of the experimental setup (a) showing the marked sections and (b) camera trap and the branch cuttings.

3.4 Measureable variables

The following site, plant and animal variables were measured and recorded in this study.

3.4.1 Site Variables

At each of the 20 plots, GPS position, season, the distance to the nearest dik-dik dung midden/game trail and the visibility of each site were recorded. Visibility (the mean distance to the nearest line-of-sight obstruction) was quantified using a range finder (Riginos & Grace, 2008). For each site visibility was measured in 4 directions (every 90° for the four cardinal directions of the compass) from the centre of the site. The rangefinder was held level at a height of about 1 m. All 4 measurements were then averaged for each habitat type. Results for the average visibility of the glades and bushland sites are included in Appendix 2.

3.4.2 Plant Variables

For every branch cutting in each plot the following were recorded:

- a) *Leaf density loss*: Two random sections of each branch cutting were marked with zip ties, one at the upper branches and one at the lower branches (Plate 3.3). The length of each marked section was measured and the number of leaves counted before and after encounters with the herbivores. The lower branches (about 50 cm from the ground) targeted dik-dik while the upper branches (about 1 m from the ground) specifically targeted impala. Two datasets were derived from this; i) the biomass density and proportion of biomass density removed, and ii) the biomass density and proportion of biomass density remaining after exposure to the foragers.
- b) *Average leaf mass*: To convert the number of leaves removed to biomass, 10 samples of each tree species leaves were taken, weighed, oven-dried, and then weighed again to get an average dry weight of a single leaf for each of the forage plant species. Given the differences in leaf sizes the number of leaves per sample varied for each tree species. For

A. brevispica and *Croton dichogamus*, each sample had 10 leaves. *A. etbaica* had 30 leaves per sample while *Grewia bicolor* had 20 leaves per sample (see Appendix 1).

3.4.3 Animal Variables

Animal responses included the number of images recorded by the camera trap for each herbivore feeding per plant. From each of the camera trap photos, the number of individuals feeding on each of the plant species for every setup were recorded. The foraging events were then compared to the type of forage and the habitat to help understand impala and dik-dik foraging behaviour in relation to predation risk and diet choice.

3.5 Data Analysis

Data analysis reflected responses of plants and animals to experimental treatments. The images from the camera traps were first quantified by going through each and every single image and recording the LMH species, the forage plant species they were feeding on, the habitat type (glade or bush), and the browsing height (lower or upper branches). Only images in which impala or dik-dik were recorded browsing on any of the four forage plants were included for data analysis. Student t-tests were used to test for differences in means. Data that did not follow the bell-shaped normality curve were first log transformed before parametric data analysis were applied.

To quantify foraging preference, the number of camera trap images taken at each plant were compared, accounting for the nested experimental design of plot within trial. From this foraging events data were generated. Foraging events were the total number of images recorded by camera traps for each herbivore (impala or dik-dik) actually feeding on the forage species. Generalized linear mixed models with a Poisson distribution were used because the response variable were counts of events. The number of images were compared by herbivore species, by tree species, by

habitat type, and by all possible two-way and three-way interactions using one way ANOVA and Tukey-HSD tests.

Leaf removal (the number of leaves removed after exposure to impala and dik-dik) were also used to quantify diet preference by comparing the biomass density and the proportion of biomass density of leaves removed for each tree species in both habitats at lower and at upper branch heights and for the whole branch cutting. Leaf removal/loss on the upper branches were equated to impala foraging while for the lower branches to dik-dik foraging. These were the actual leaf biomass eaten by impala and dik-dik. Linear-mixed effects models were used to test for the effects of habitat type on the leaf removal, in upper and lower branches and for the whole tree.

To quantify the effectiveness of plant defence against herbivory by impala and dik-dik, leaf survival (leaves remaining after exposure to the herbivores), the biomass density and the proportion of biomass density of leaves remaining were compared for each tree species in both habitats, at lower and upper branch heights and for the whole branch cuttings. Linear-mixed effects models were again used to test for the effects of habitat type on the leaf removal, both in upper and lower branches. Leaf survival was equated to the effectiveness of the plant defences against herbivory by impala and dik-dik. The higher the number or biomass density remaining after visitation by the herbivores, the more effective the plant defences possessed by the tree species.

All statistical analyses were performed using the “nlme” (Pinheiro *et al.*, 2015), ‘lme4’ (Bates *et al.*, 2015) and ‘glmmADMB’ packages (Fournier *et al.*, 2012) in R version 3.2.2 (R Core Team 2015) and significance was determined at the level of $P < 0.05$.

Chapter 4 : Results

4.1 Visibility in the Glades and Bushland

There were significant differences in mean visibility in bush and glades ($t = -7.52$, $df = 18.78$, p -value < 0). Mean visibility in the glades was $71.5 (\pm 7.78)$ m while for bush visibility reduced to $12.38 (\pm 1.14)$ m (Appendix 2).

4.2 Foraging Events from Camera traps

A total of 25,172 foraging events were recorded for both impala and dik-dik in the open and bushland habitats. Of these, 16,006 were recorded in the open while 9,166 were recorded in the bushland. Approximately 54.35% more foraging events occurred in the open habitats than the bushland. Impala recorded 15,865 foraging events in the open habitat and 8,429 in bushland, while dik-dik recorded 141 and 737 in the open and bushland habitats respectively. Impala recorded 16,533 foraging events for leaves on the upper branches while dik-dik only recorded 26 foraging events. On the lower branches, impala recorded 7,761 and dik-dik 852 foraging events.

There were significant effects of herbivore species, habitat type, and plant species on foraging preferences. In overall *Grewia bicolor* and *A. brevispica* were browsed more, both in the open and in the bushland, whereas *A. etbaica* and *Croton* were browsed the least (Figure 4.1). Summary of the foraging events data are included in Appendix 3.

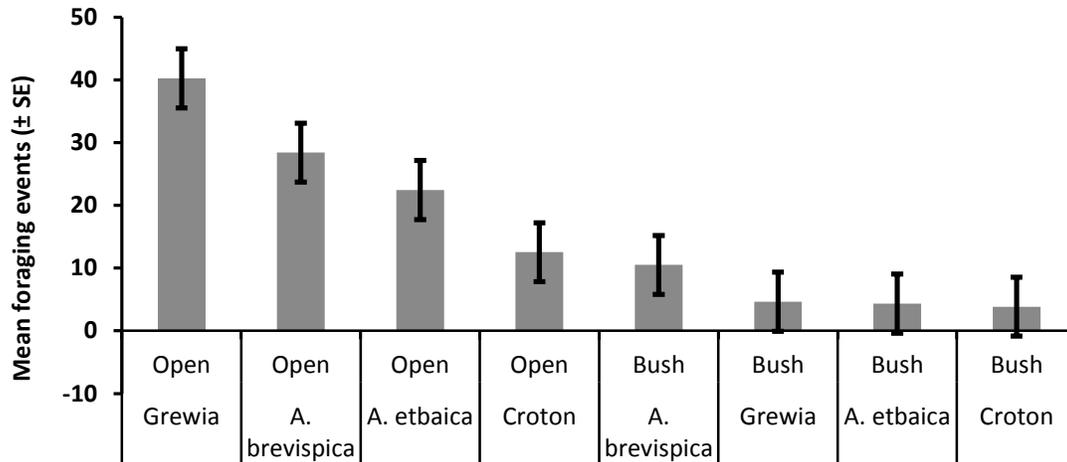


Figure 4.1 Combined mean foraging events for impala and dik-dik in open and bush habitats.

4.2.1 Impala Foraging Preference as Determined by Foraging Events

Impala recorded higher mean foraging events in open habitats than in bushland ($t = -6.276$, $df = 378.53$, $p\text{-value} < 0.01$), with the exception of *Grewia bicolor* (Table 4.1). They recorded 50.65% more mean foraging on the upper branches than on the lower branches ($t = -7.133$, $df = 401.91$, $p\text{-value} < 0.001$). Tukey post-hoc multiple comparison analysis for the same plant species in different habitats for impala were < 0.05 except for *Grewia bicolor* (Table 4.1). Impala's foraging preference did not significantly vary by plant species in the glades (open habitat) (Table 4.1) while in the riskier bushland sites, impala significantly browsed more on the less-thorny *A. brevispica* than *A. etbaica* (Table 4.1). Impala recorded the second highest mean foraging events for the thornless *Grewia bicolor* in the bush (Figure 4.2). Impala diet preference in the bush ranked from *A. brevispica* to *Grewia bicolor*, to *Croton dichogamus* and to *A. etbaica* in that order (Figure 4.2).

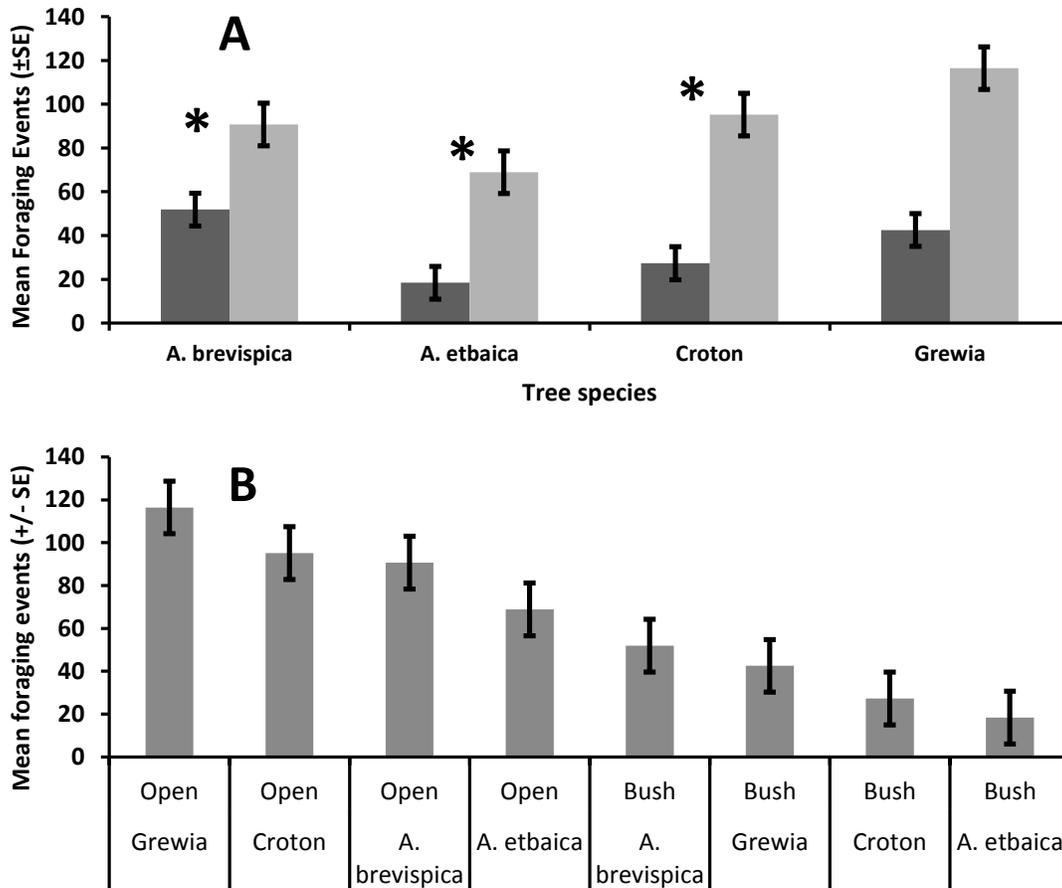


Figure 4.2 Mean foraging events for impala recorded by camera traps. Asterisks (*) indicate significance at $p=0.05$ between the open and bushland habitats. Grey bars in (A) represent open (glades) while black bars represent bushland habitats

4.2.2 Dik-dik Foraging Preference as Determined by Foraging Events

Dik-dik mean foraging events were higher in the bushland than in the open habitat ($t = 4.356$, $df = 394.34$, $p\text{-value} < 0.01$) (Figure 4.3). They exclusively foraged on the lower branches (185.76% more) than on the upper branches ($t = 8.527$, $df = 222.98$, $p\text{-value} < 0.001$) and preferred foraging on *A. etbaica* and *A. brevispica* compared to *Grewia bicolor* or *Croton dichogamus* (Figure 4.3, Table 4.1). They showed high preference for the thorny *A. etbaica*, even in the open habitat where they perceive as risky (Figure 4.3). Dik-dik were never recorded by camera traps feeding on *Croton dichogamus* in the glades.

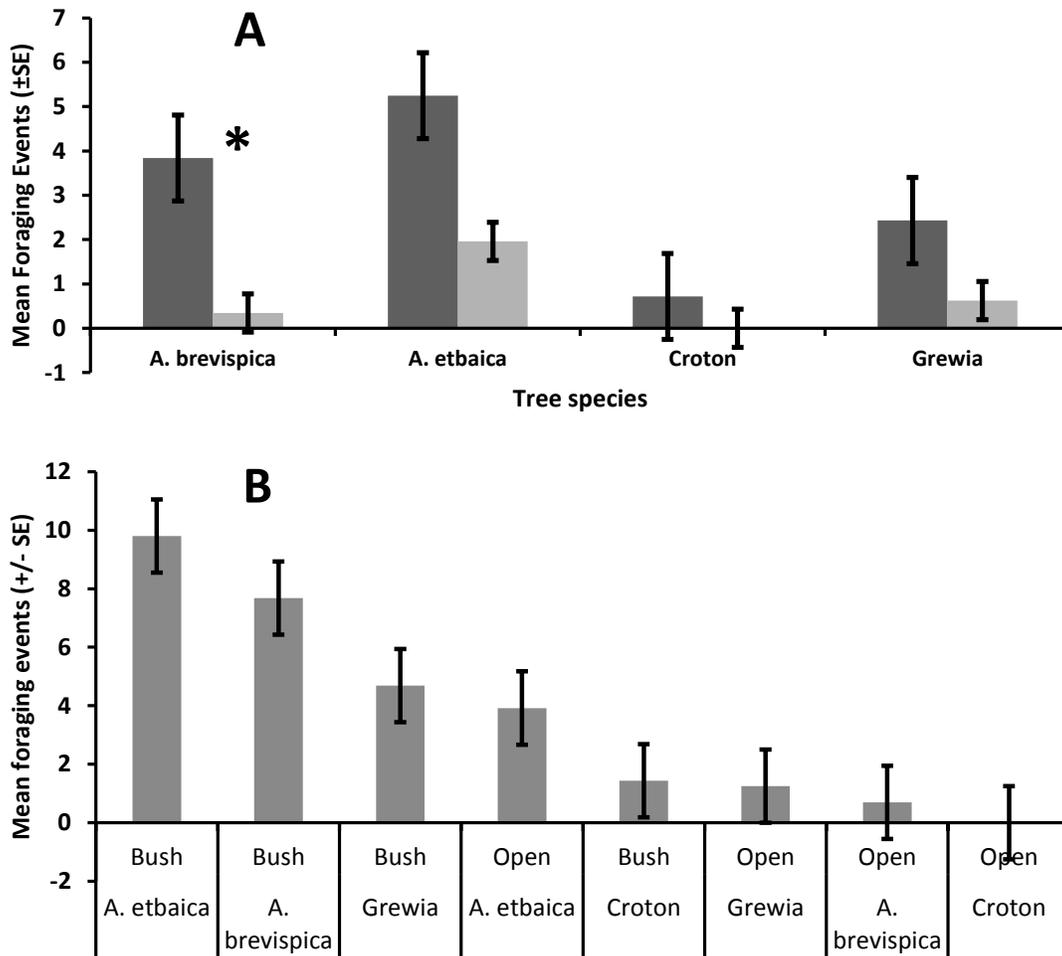


Figure 4.3 Mean foraging events for dik-dik recorded by camera traps. Asterisks (*) indicate significance at $p=0.05$ between the open and bushland habitats. Grey bars in (A) represent open (glades) while black bars represent the bushland habitats.

4.2.3 Comparing Foraging Events of Impala and Dik-dik

Within the open habitats, there were significant differences between impala and dik-dik (within the same habitat type and forage species) foraging for *A. brevispica* and *Grewia* (p -value < 0.01 for both. See Table 4.1). However, in bushland, there were no significant differences between foragers for *A. brevispica*, *A. etbaica*, and *Croton dichogamus*. Likewise, for *A. etbaica* in the open there were no significant differences between the herbivores (Table 4.1).

Table 4.1 Post hoc multiple comparison of means using Tukey HSD test for impala and dik-dik foraging events. Comparisons involving dik-dik and *Croton dichogamus* foraging events in the open are excluded because dik-dik were not recorded browsing on *Croton* in the open habitat. Significantly different combinations are marked with asterisks (*).

Herbivore	Comparison	Habitat type	Tree species	Mean difference (±SE)	Z value	P value
Impala	Habitat type	Open vs. bushland	<i>A. brevispica</i>	1.371 (±0.324)	4.236	0.001*
			<i>A. etbaica</i>	2.784 (±0.525)	5.303	0.001*
			<i>Croton</i>	1.501 (±0.486)	3.090	0.037*
			<i>Grewia</i>	0.774 (±0.474)	1.633	0.693
Dik-dik	Habitat type	Open vs. bushland	<i>A. brevispica</i>	-2.924 (±0.820)	-3.565	0.006*
			<i>A. etbaica</i>	-1.382 (±1.050)	-1.316	0.815
			<i>Grewia</i>	-2.514 (±1.123)	-2.238	0.246
Impala	Trees	Open	<i>A. etbaica</i> vs <i>A. brevispica</i>	-0.054 (±0.482)	-0.111	1.000
			<i>Croton</i> vs <i>A. brevispica</i>	-0.612 (±0.519)	-1.180	0.922
			<i>Grewia</i> vs <i>A. brevispica</i>	0.589 (±0.482)	1.221	0.908
			<i>Croton</i> vs <i>A. etbaica</i>	-0.558 (±0.540)	-1.035	0.960
			<i>Croton</i> vs <i>Grewia</i>	0.643 (±0.477)	1.346	0.856
Impala	Trees	Bush	<i>A. etbaica</i> vs <i>A. brevispica</i>	-1.467 (±0.362)	-4.049	0.001*
			<i>Croton</i> vs <i>A. brevispica</i>	-0.743 (±0.309)	-2.400	0.217
			<i>Grewia</i> vs <i>A. brevispica</i>	0.031 (±0.359)	0.087	1.000
			<i>Croton</i> vs <i>A. etbaica</i>	0.725 (±0.478)	1.517	0.766
			<i>Grewia</i> vs <i>A. etbaica</i>	1.498 (±0.518)	2.894	0.065
Dik-dik	Trees	Open	<i>A. etbaica</i> vs <i>A. brevispica</i>	2.683 (±1.197)	2.241	0.244
			<i>Grewia</i> vs <i>A. brevispica</i>	0.451 (±1.085)	0.416	0.999
			<i>Croton</i> vs <i>Grewia</i>	-2.231 (±1.150)	-1.940	0.413
Dik-dik	Trees	Bush	<i>A. etbaica</i> vs <i>A. brevispica</i>	1.140 (±0.677)	1.683	0.586
			<i>Croton</i> vs <i>A. brevispica</i>	-1.044 (±0.797)	-1.309	0.819
			<i>Grewia</i> vs <i>A. brevispica</i>	0.041 (±0.687)	0.059	1.000
			<i>Croton</i> vs <i>A. etbaica</i>	-2.184 (±1.114)	-1.960	0.401
			<i>Grewia</i> vs <i>A. etbaica</i>	-1.099 (±0.980)	-1.122	0.903
			<i>Grewia</i> vs <i>Croton</i>	1.084 (±0.983)	1.103	0.909
Impala vs Dik-dik	Trees	Open	<i>A. brevispica</i>	5.234 (±1.024)	5.111	0.010*
			<i>A. etbaica</i>	3.481 (±1.152)	3.022	0.115
			<i>Grewia</i>	5.382 (±1.126)	4.780	0.010*
Impala vs Dik-dik	Trees	Bush	<i>A. brevispica</i>	1.642 (±0.717)	2.290	0.518
			<i>A. etbaica</i>	-1.651 (±1.350)	-1.223	0.992
			<i>Croton</i>	2.468 (±1.038)	2.377	0.453
			<i>Grewia</i>	0.884 (±0.977)	0.904	0.999

4.3. Foraging Preference as Determined by Leaf Biomass Density Removed

Summary of leaf biomass density and the proportion (%) of biomass density removed by impala and dik-dik are appended in Appendix 4 and Appendix 5 respectively.

4.3.1 Impala Foraging Preference from Leaf Biomass Density Removed

For leaves on the upper branches, there were no significant difference between the mean biomass density of leaves removed in the open and bushland habitats for all the tree species except *A. brevispica* ($F(1, 59) = 4.592$, $p\text{-value} = 0.036$) (Figure 4.4a, Appendix 4). But the proportion (%) of biomass density removed only showed significant difference between the habitats for *Grewia bicolor* ($F(1, 52) = 6.415$, $p\text{-value} = 0.014$) (Figure 4.4b, Appendix 5). *Grewia bicolor* and *A. brevispica*, were browsed the most, both in the open and bushland habitats (Figure 4.4c). *A. etbaica* was the least browsed by impala in the open bush while *Croton dichogamus* was avoided by impala in both habitats (Figure 4.4c).

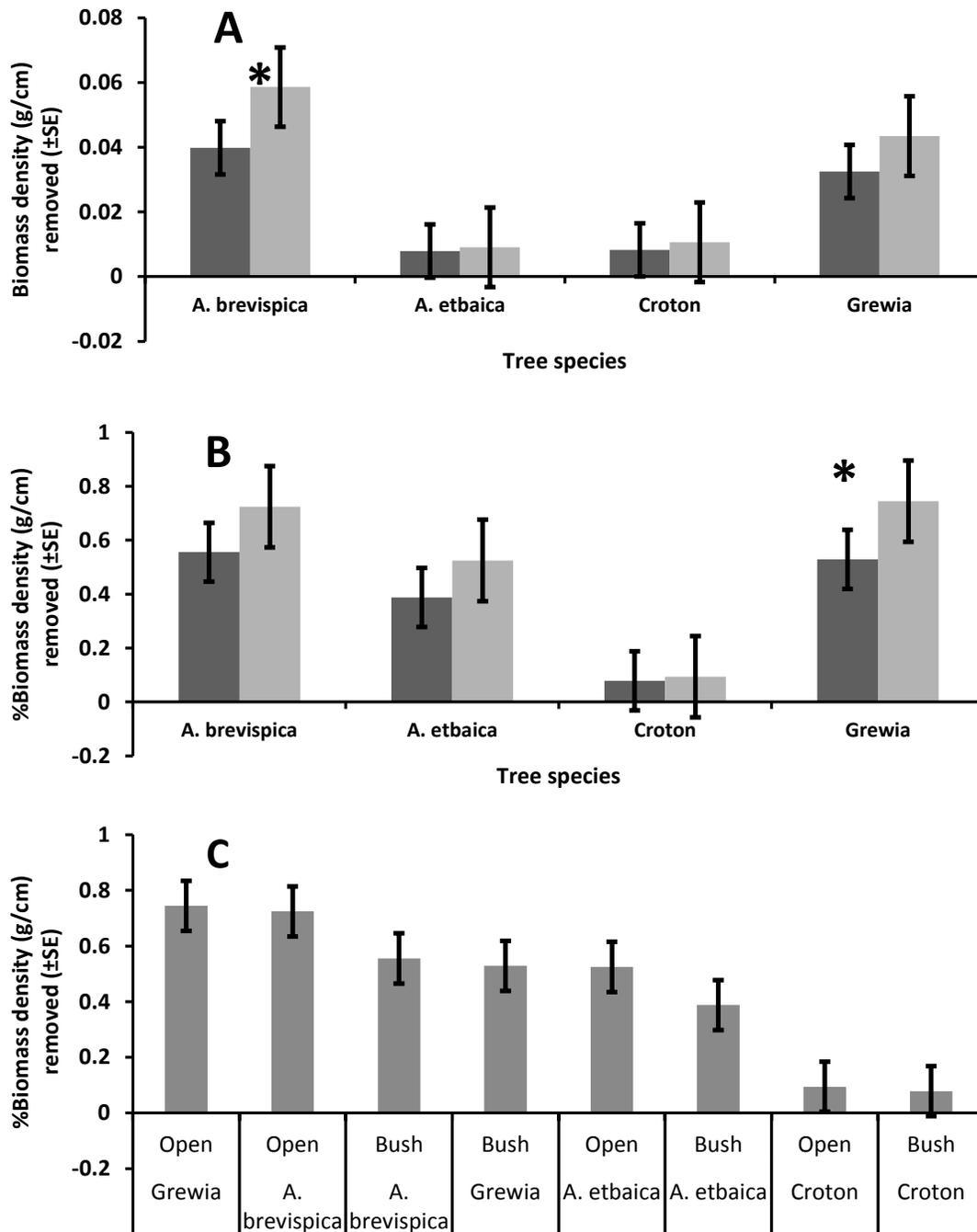


Figure 4.4 Mean biomass density (A) and the proportion of biomass density (B) of leaves removed by impala. Black bars represent bushland while the grey bars represent open (glade) habitats. Asterisk (*) indicate significant differences between the habitats.

4.3.2 Dik-dik Foraging Preference from Leaf Biomass Density Removed

There were no effect of habitat type on the biomass density of leaves removed on the lower branches for all the tree species except for *Grewia bicolor* ($F(1, 52) = 4.086$, $p\text{-value} = 0.048$) (Figure 4.5a, Appendix 4). The proportion (%) of biomass density of leaves removed on the lower branches were not affected by habitat type for all the tree species (See Appendix 5). Foraging on the lower branches was mainly done by dik-dik. In the open dik-dik browsed more on *Grewia dichogamus* and *A. brevispica* while in the bush higher proportion of biomass density was removed for *A. etbaica* (Figure 4.5c). *Croton dichogamus* recorded the least proportion of biomass density removed in both habitats (Figure 4.5c).

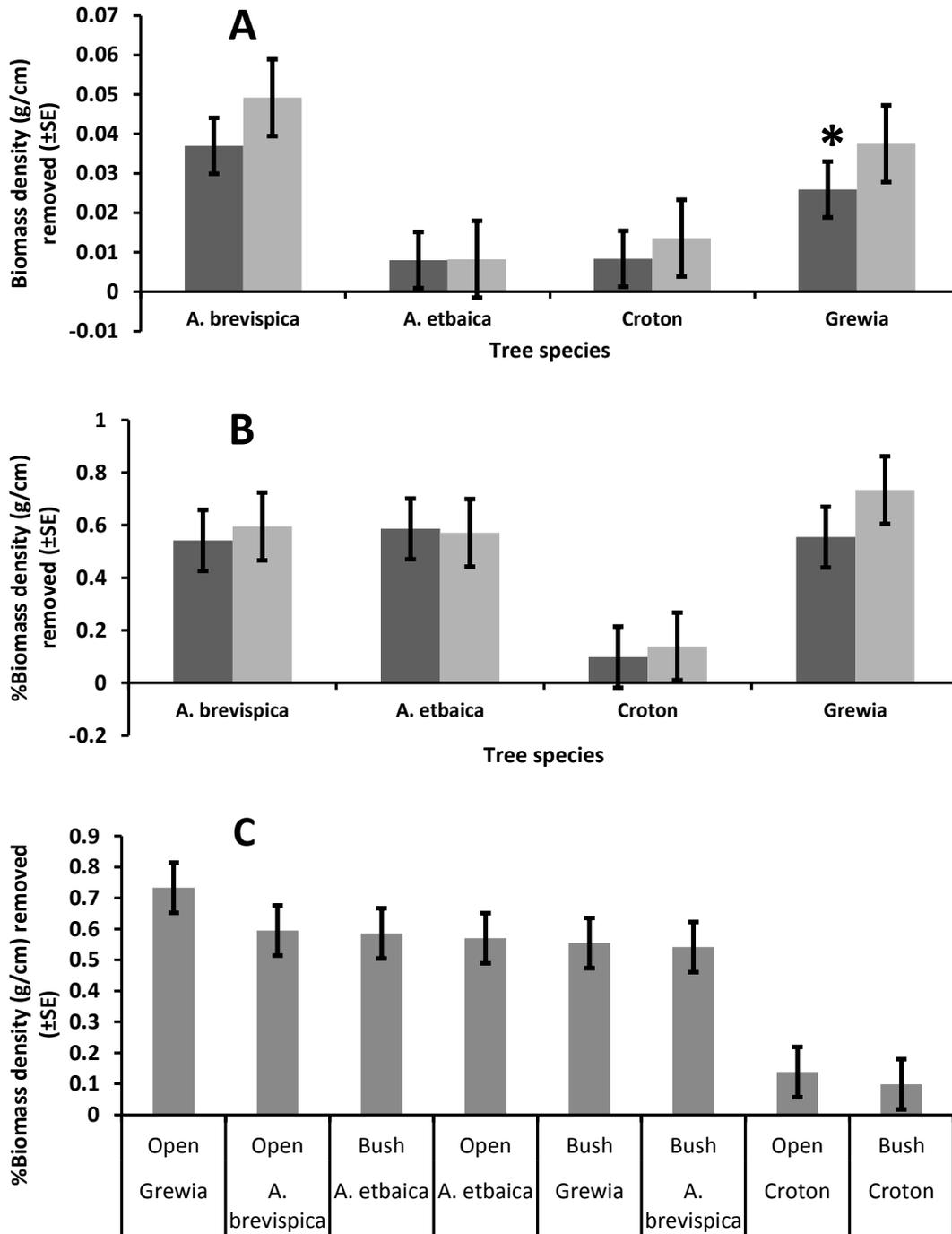


Figure 4.5 Mean biomass density (A) and the proportion of biomass density (B) of leaves removed by dik-dik. Black bars represent bushland habitats while grey bars represent

open habitat. Asterisk (*) indicate significant differences between open and bushland habitat.

4.3.3 Leaf Biomass Density Removed by both Impala and Dik-dik

When leaf removal for both leaves on the lower and upper branches (the whole tree) were compared, habitat effect on the biomass density and the proportion (%) of biomass density of leaves removed were only significant for *A. brevispica* $F(1, 59) = 4.268$, $p\text{-value} = 0.043$) and *Grewia bicolor* ($F(1, 52) = 4.871$, $p\text{-value} = 0.032$) (Figure 4.6: See Appendix 4 and 5). *Grewia bicolor* and *A. brevispica* were browsed the most while *A. etbaica* were browsed the least, both in the open and bushland habitats (Figure 4.6c). *Croton* recorded the least proportion of biomass density removed in both habitats (Figure 4.6c). The per capita (per leaf) risk of herbivory from impala and dik-dik increased from plants in the bush to the plants in the open habitat, and from plants without or with minimal physical (thorns) defence to plants with higher physical defences (Figure 4.6c).

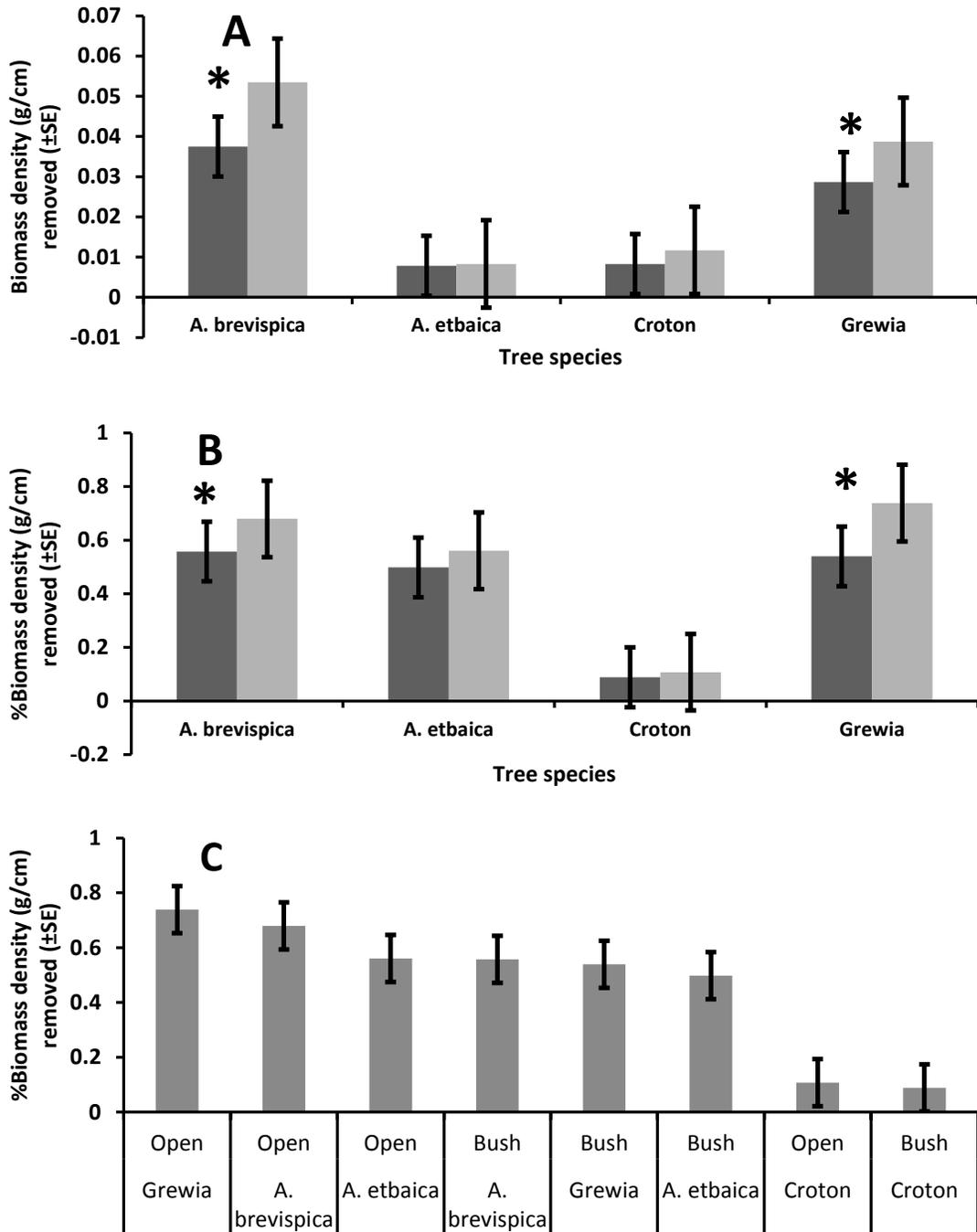


Figure 4.6 Mean biomass density (A), the proportion of biomass density (B), and the ranking of the proportion of biomass density removed (C) by impala and dik-dik. Asterisk (*) indicate significant differences between open and bushland habitat.

4.4 Efficacy of Plant Defences

Leaf survival was the number of leaves remaining after exposure to the herbivores. Leaf biomass density remaining and proportion of leaf biomass density remaining on the upper branches was used to determine the effectiveness of the plant defences against impala herbivory and on the lower branches to determine plant defence efficacy against herbivory by dik-dik.

4.4.1 Efficacy of Plant Defences against Herbivory by Impala

The mean biomass density of leaves remaining on the upper branches (Figure 4.7a) were significantly higher in bush than open habitats for *A. brevispica* ($F(1, 59) = 4.768$, p -value = 0.033), *A. etbaica* ($F(1, 67) = 6.404$, p -value = 0.014), and *Grewia bicolor* ($F(1, 52) = 8.492$, p -value = 0.005), but not for *Croton dichogamus* ($F(1, 57) = 0.006$, p -value = 0.939) (See Appendix 6). On the other hand the proportion (%) of biomass density remaining only showed effect of habitat type for *A. etbaica* ($F(1, 67) = 4.057$, p -value = 0.048) and *Grewia bicolor* ($F(1, 52) = 11.455$, p -value = 0.001) (Figure 9b, Appendix 7). In overall, *Croton dichogamus* and *A. etbaica*, both in the open and bush, recorded the highest proportion of biomass density remaining while *Grewia bicolor* and *A. brevispica* in the open recorded the least biomass density remaining (Figure 4.7b).

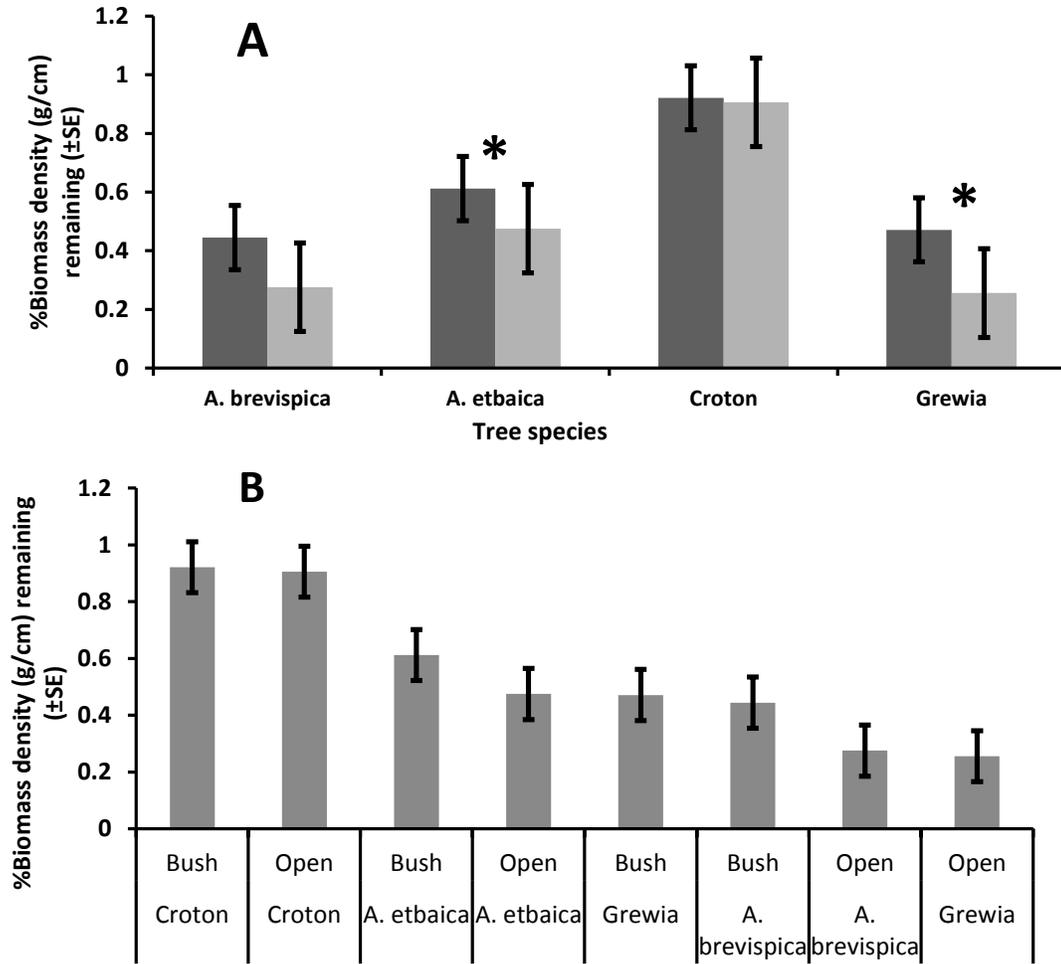


Figure 4.7 Proportion of biomass density of leaves remaining and the ranking of the proportion of biomass density remaining after exposure to impala in the open (grey bars) and bushland (black bars) habitats.

4.4.2 Efficacy of Plant Defences against Herbivory by Dik-dik

There were no significant effect of habitat type on the biomass density and proportion (%) of biomass density of leaves remaining on the lower branches for all the four forage species after exposure to dik-dik (Figure 4.8a; See Appendix 6 and 7). However, *Croton dichogamus* recorded the highest biomass density remaining in both bush and open habitats while *Grewia bicolor* recorded the least in open habitat (Figure 4.8b). In the bush *A. etbaica* defences were the least effective against dik-dik browsing while in the open *Grewia bicolor* and *A. brevispica* defences

were the least effective as these recorded the least proportion (%) biomass density remaining (Figure 4.8b).

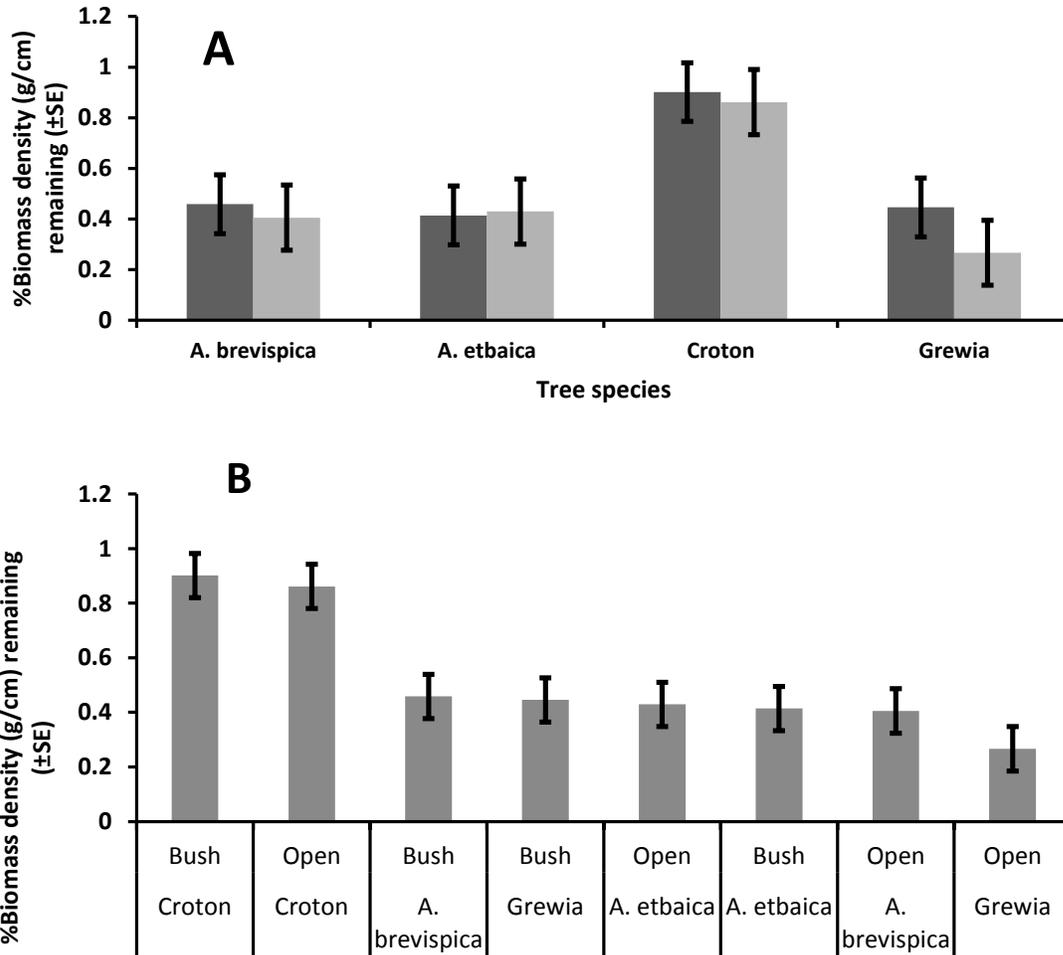


Figure 4.8 Proportion of biomass density of leaves remaining (B) and the ranking (C) of the proportion of biomass density remaining after exposure to dik-dik in the open (grey bars) and bushland (black bars) habitats.

4.4.2 Efficacy of Plant Defences against Herbivory by Impala and Dik-dik

There were no significant differences in the biomass density and proportion of biomass density remaining between the glades and bushland for all the forage tree species except for *Grewia bicolor* (*A. brevispica* $F(1,59) = 1.458$) $p=0.232$, *A. etbaica* $F(1,67) = 1.969$) $p=0.165$, *Croton*

dichogamus $F(1,52) = 0.319, p=0.574$, *Grewia bicolor* $F(1,52) = 9.542, p=0.003$). There were 55.18% more of *Grewia bicolor* remaining in bush than in glades.

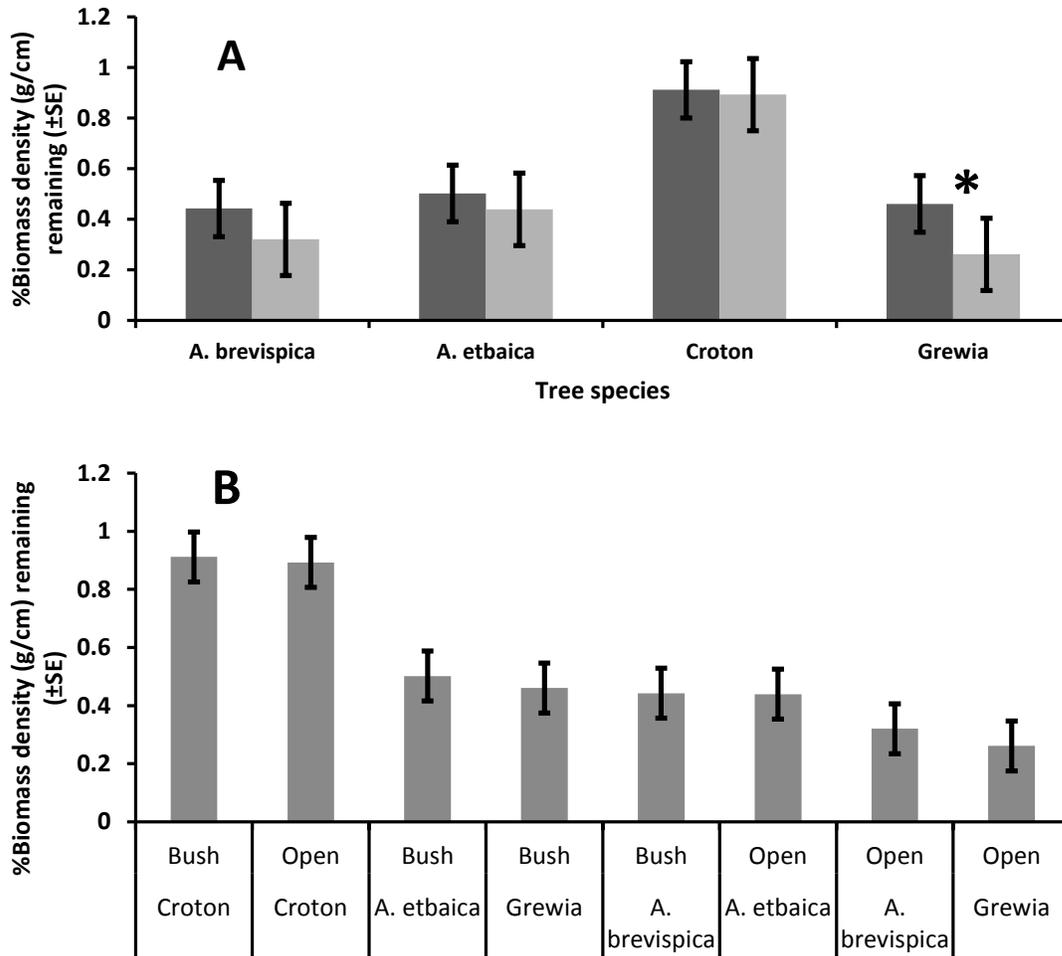


Figure 4.9 Proportion (%) of mean biomass density remaining after exposure to both impala and dik-dik.

Chapter 5 : Discussion

5.1 Discussion

5.1.1 Foraging Preference

Results show that impala generally foraged more in the glades where they perceived as less risky. The grasses in the glades are rich in nutrients and has been posited to be the reason why impalas are attracted to these habitats (Augustine, 2004). But Ford *et al.* (2014) showed that the primary reason impalas frequent glades is to avoid predation as predators are known to use bush cover to conceal themselves when hunting (Underwood, 1982; Hopcraft *et al.*, 2005; Riginos & Grace, 2008; Anderson *et al.*, 2010; Thaker *et al.*, 2011; Valeix *et al.*, 2011). Because ungulates live in a 'landscape of fear' (LOF) (Laundre *et al.*, 2001) and tend to avoid those habitats they perceive to be risky, impala avoided bushland but frequented the open habitats (van der Merwe & Brown, 2008; Iribarren & Kotler, 2012; Ford *et al.*, 2014; Laundre *et al.*, 2014). This is evident by the comparatively higher foraging events recorded by the camera traps in the glades and the mean leaf biomass density removed by impala (upper branches) in the glades.

However, this was not the case for the small-bodied dik-dik, whom like other smaller-bodied LMH, rely on cryptic behaviour to avoid predators (Jarman, 1974). Dik-dik LOF was quite the opposite of impala and they have been known to spend most of their time in the bushland (Ford & Goheen, 2015). Both impala and dik-dik recorded higher foraging in the habitats they perceived as less risky and in these habitats they had more foraging time per tree species. This was in line with the predictions under risk-driven hypotheses, where the LMH were predicted to record more foraging in habitats they perceived as safe and more selective in risky habitats. Increasing access time for resources lead to more foraging events in the safe habitats, for both impala and dik-dik

and this has also been recorded in other studies for rodents (Brown, 1988), for primates (Cowlshaw, 1997), for birds (Carrascal *et al.*, 2006) and for herbivores (Valeix *et al.*, 2009).

Impala while in the risky bushland habitat foraged more on plants that were relatively easier to ingest: the less-thorny *A. brevispica* and the thorn-less *Grewia bicolor*. They however, foraged less on the thornier *A. etbaica* and avoided *Croton dichogamus*. *A. brevispica* has only short spines compared to *A. etbaica* that has both short and long spines. *Grewia bicolor* lack the thorns altogether. Spines are form of mechanical plant defence and they act by reducing ingestion of leaves by the herbivores (du Toit 2003; Borchard *et al.*, 2011) thus ingesting leaves of *Grewia bicolor* and *A. brevispica* would be relatively much easier and faster than ingesting leaves of *A. etbaica*. Ford *et al.* (2014) showed that impala avoided *A. etbaica* because of the long spines and when the long spines were removed and added to *A. brevispica* their foraging on *A. etbaica* was tremendously increased. The study illustrated the importance of spines and thorns on the ingestion of plants by impalas in a savannah ecosystem. Because the risk of predation for impala is greater in the bushland they needed to allocate more time scanning for predators and thus they chose to forage on plants that were easier and faster to ingest. *Croton dichogamus* though does not have any prominent form of mechanical defence, must have had a relatively strong chemical defence (Young *et al.*, 1998 Hemayet *et al.*, 2012) and so was foraged on the least by impala, both in glades and in the bushland. This implies that the effect of *Croton dichogamus* chemical defence is way much higher than the nutritional value the LHM would derive from these leaves.

Dik-dik, just like impala, also browsed more in the habitat they perceived as "safe" (bushland) and lesser in the "risky" habitat (glades). They however, preferred the thorny *A. etbaica* and *A. brevispica* to the thorn-less *Grewia bicolor* and *Croton dichogamus*. With their nimble mouthparts, smaller LMH are better equipped to avoid plant mechanical defence than the larger LMH. Dik-dik

were able to navigate around the thorns to reach the leaves of *A. etbaica* and *A. brevispica* more easily than impala.

Both impala and dik-dik avoided *Croton dichogamus* in both habitats. High concentrations of tannins are known to reduce voluntary feed intake and nutrient digestibility, whereas low to moderate concentrations have nutritional benefit for herbivores by protecting dietary proteins from excessive ruminal degradation without affecting forage intake or fibre digestion (Barry *et al.*, 1986; Frutos *et al.*, 2004). Although doing bioassays for the chemical contents of the forage plants was beyond the scope of this study, *Croton dichogamus* has been recorded elsewhere to have a higher tannin content (Hemayet *et al.*, 2012) making it less nutritionally important. Tannin content for *Grewia* spp leaves have been recorded in other studies to be less than tannin content for *Croton* spp (Apori *et al.*, 1998; Hemayet *et al.*, 2012). Ford *et al.* (2014) experimentally showed that for *A. brevispica* and *A. etbaica* mechanical defences were more important in influencing their herbivory. In removing the long thorns on *A. etbaica* and adding them to *A. brevispica* impalas increased their foraging on the thorn-removed *A. etbaica* but reduced their consumption of the thorn-addition *A. brevispica*. This demonstrated that for *A. etbaica* and *A. brevispica* mechanical defences were the limiting factor for LMH feeding on them. This was also supported in this study: Dik-dik despite *A. etbaica* being highly mechanically defended they still recorded higher foraging for it because with their nimble mouth parts the thorns were not effective in deterring herbivory against them.

All in all, these results support the palatability-driven hypothesis prediction that chemical defences would be more effective against smaller-bodied LMH and because gut capacity decreases with body size larger guts are needed to overcome the effect of chemical defences once ingested. Thus diet preference for dik-dik was more constrained by plant chemical defences rather than

mechanical defences and they would even trade-off some risk to get to *A. etbaica* in the risky habitat (glades).

5.1.2 Efficacy of Plant Defences against Herbivory by Impala and Dik-dik

The biomass density of leaves remaining on the trees after exposure to impala and dik-dik reflected on the effectiveness of plant defences against herbivory. The higher the GUD (biomass density remaining) the more effective the plant defences were against herbivory by the LMH. Overall, the thorn-less *Croton dichogamus* defences were the most effective against impala and dik-dik herbivory, both in the glades and in the bush, followed by *A. etbaica* in the bush. Despite *Croton dichogamus* lacking the mechanical defences like thorns and spines, their tannin content must have been high enough (Hemayet *et al.*, 2012) to render them nutritionally unimportant to herbivores regardless of which habitat they were (Barry *et al.*, 1986; Young *et al.*, 1995; Frutos *et al.*, 2004). But because this study did not conduct chemical bioassays for the forage plant species, probably some factors other than tannin content could have contributed to the higher GUD for *Croton dichogamus* in both habitats. However, plants have been shown not to invest in both mechanical and chemical defences (Moles *et al.*, 2013; Ward & Young, 2002) and thus the lack of spinescence in *Croton dichogamus* and *Grewia bicolor* makes them more likely to have invested in chemical defences and the vice versa for *A. etbaica* and *A. brevispica*. The long spines of *A. etbaica* has been shown to reduce herbivory (Ford *et al.*, 2014) and given that impala perceive bush as risky *A. etbaica* would take them longer to ingest (Cooper & Owen-Smith, 1986; Belovsky *et al.*, 1991; Gowda 1996) and yet they needed to allocate more time in predation avoidance behaviour such as scanning for predators. But while in the safer habitat (glades), impala had time allocated for browsing and so they managed to at least browse on *A. etbaica*.

Though *A. etbaica* defences were effective against impala, especially in bushland, for dik-dik *A. etbaica* was the least effective in both habitats. Due to the allometric gut capacity scaling, mechanical defences are less effective against the smaller-bodied LMH as they are able to navigate around the thorns and spines to get to the leaves of mechanically defended plants. Some studies comparison. Larger-bodied LMH species, like impala, are known to require higher densities of nutrients in their food but less total plant material and due to their large gut capacity are able to digest coarse and more toxic plant materials (Underwood, 1982; Ritchie & Olf 1999; Borchard *et al.*, 2011).

When looking at the efficacy of plant defences against herbivory by both impala and dik-dik, *Croton dichogamus* and *A. etbaica* defences in the bush and glade were the most effective (fewer GUD), while *A. brevispica* and *Grewia bicolor* defences in glades were the least effective (comparatively more GUD) against herbivory. *A. brevispica* and *A. etbaica* both has thorns but the latter (*A. etbaica*) has got both the short and long spines making it the most mechanically defended than *A. brevispica*. While on the other hand *Croton* species have been recorded to have higher tannin content compared to *Grewia* species (Apori *et al.*, 1998; Hemayet *et al.*, 2012) making *Croton* spp highly chemically defended. From this, a clear pattern emerges where plants with better mechanical or chemical defences have higher chances of escaping herbivory from LMH than plants with less or without defences and this is in support of the palatability driven and accessibility driven foraging hypotheses.

Chapter 6 : Conclusion and Recommendation

6.1 Conclusion

From the herbivore's perspective, the risk of predation is more important than forage preference. Higher foraging events and density of biomass removal for impala were all in the safer habitats, (glades), and they were more selective in the bush. Impala preferred the less mechanically defended *A. brevispica* and the thorn-less *Grewia* in bush but showed no preference while in the glades. Dik-dik on the other hand, recorded the highest foraging events and density of biomass removal in the bush and showed preference for the thorny *A. etbaica* even in the riskier open habitats. For dik-dik the effect of chemical defences is more important than mechanical defences and so they would rather trade off some risk to get the highly mechanically defended *A. etbaica* in the risky habitat (glades).

From the plants perspective, defences are more important than habitat and thus plants with better mechanical or chemical defenses have higher chances of escaping herbivory from impala and dik-dik irrespective of the habitat in which they are.

6.2 Implication to Ecology and Management

Anthropogenic activities exert a major influence on the interaction between carnivores, herbivores and the vegetation communities in a savannah ecosystem. Glades are as a result of livestock husbandry practices (Young *et al.*, 1995) and they provide a mosaic that has shaped the spatial foraging patterns of LMH (Ford *et al.*, 2014). With the loss of carnivores, for instance, landscapes are more likely to become less risky (Berger *et al.*, 2001) decoupling the spatial interplay of risk avoidance and diet selection. Loss of carnivores will also render obsolete the need for pastoralists to corral their livestock in bomas at night, eliminating the formation of glades and thus the risk

heterogeneous landscape. Human-driven loss of large carnivores from African savannahs (Estes *et al.*, 2011) will reduce spatial variation in plant communities (Ford *et al.*, 2014) and only plants equipped with better defences against herbivory are likely to survive. Again with effects of the imminent climate change such as shrub encroachment (increase of woody plant cover) into formerly open and grassy areas (Archer *et al.*, 1995), glades are likely to be eliminated making this ecosystem homogenous in terms of land cover. This study illustrate the important role pastoralists, in the presence of carnivores, play (indirectly) in the spatial interplay of risk avoidance, diet selection and tree distribution within the Savannah ecosystem.

6.2 Study Limitation and Recommendations

One important limiting aspect of this study was the lack of comparative bioassays of chemical composition for the four forage plant species. The study relied more on the secondary data from other studies of which not a single one had chemical composition (more so tannin content) for all the forage plant species in this study. Though there are almost non-existent studies on the nutritional and tannin content for all the four study forage species there was at least for *Grewia* spp (e.g Apori, *et al.*, 1998), *Croton* spp (e.g Hemayet *et al.*, 2012), and *A. brevispica* (e.g Abdulrazaak *et al.*, 2000), but none for *A. etbaica*. Even though thorns and spines are more important as plant defences against herbivory for mechanically defended plants (*A. brevispica* and *A. etbaica*) it would still be very valuable and informative to look into how nutritional and chemical composition vary across these forage species. It is therefore highly recommended that any future study looking into how plant defences, especially chemical defences, influence foraging behaviour of herbivores should incorporate the aspect of bioassay analysis. This is so because, there are no known studies up to date that have looked into how the combined effect of chemical or mechanical defences, nutritive value, and the risk of predation influence foraging behaviours of wild herbivores. This study, in particular, only looked at the interaction of mechanical defences and “perceived” chemical defences, coupled with predation risk on foraging behaviour of LMH, but never looked into detail the influence of nutritional value and chemical content, more so tannin content, on diet choice.

Another interesting aspect to look into in the future studies would be how predation risk and plant defences influence the foraging preference of herbivores larger (<50) than impala (e.g buffaloes) and the mega-herbivores (e.g giraffes, elephants) given that their LOF is different from those of

impala and dik-dik and the mega-herbivores are likely to escape both plant defences and predation (Sinclair *et al.*, 2003).

It is evident that livestock husbandry practices influences the heterogeneity of the savannah landscapes (Young *et al.*, 1995; Augustine 2004) and this in turn influences the distribution of trees (Ford *et al.*, 2004) and the diet choice of LMH. It is therefore paramount for the rangeland managers to recognize that placement and relocation rate of bomas has influence on the foraging behaviour and diet choice of LMH across a spatial gradient.

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Appendices

Appendix 1. Average Leaf Weight for the Forage Tree Species Used in the Study.

Tree Species	Mean Leaf Weight (g)	StDev	N	SE	No of leaves per sample
<i>Acacia brevispica</i>	0.1443	0.0281	10	0.0089	10
<i>Acacia etbaica</i>	0.0117	0.0017	10	0.0005	30
<i>Croton dichogamus</i>	0.1383	0.0196	10	0.0062	10
<i>Grewia bicolor</i>	0.0383	0.0102	10	0.0032	20

Appendix 2. Average Visibility (m) in Bush and glade habitats

Habitat	Mean Visibility (m)	N	StdDev	SE
Bush	12.38*	38	7.04	1.14
Glade	71.50*	19	33.90	7.78

* Significant differences in mean visibility in bush and glades ($t = -7.52$, $df = 18.78$, $p\text{-value} < 0$).

Appendix 3. Summary of Foraging Events Recorded by Camera traps for Impala and Dik-dik.

Impala	Mean		Count		Stdev		SE		P-value (Tukey test)
	Bush	Open	Bush	Open	Bush	Open	Bush	Open	
<i>A. brevispica</i>	51.887	90.673	62	52	78.344	135.954	9.950	18.853	< 0.001
<i>A. etbaica</i>	18.433	68.920	60	50	58.067	132.075	7.496	18.678	< 0.001
<i>Croton dichogamus</i>	27.333	95.188	60	32	29.846	101.197	3.853	17.889	0.037
<i>Grewia bicolor</i>	42.517	116.450	58	40	68.254	138.860	8.962	21.956	0.693

Dik-dik	Mean		Count		Stdev		SE		P-value (Tukey test)
	Bush	Open	Bush	Open	Bush	Open	Bush	Open	
<i>A. brevispica</i>	3.839	0.346	62	52	11.333	1.413	1.439	0.196	0.006
<i>A. etbaica</i>	5.250	1.960	60	50	10.809	6.803	1.395	0.962	0.815
<i>Croton dichogamus</i>	0.717	0.000	60	32	2.248	0.000	0.290	0.000	#
<i>Grewia bicolor</i>	2.431	0.625	58	40	5.252	1.944	0.690	0.307	0.246

No dik-dik was recorded by the camera traps feeding on *Croton dichogamus* in the open (glade) habitats.

Appendix 4. Summary Statistics for Biomass Density (g/cm) removed by Impala and Dik-dik

Upper branches (Impala)	Mean		Stdev		N		SE		P-Values	ANOVA Statistics
	Bush	Open	Bush	Open	Bush	Open	Bush	Open		
<i>A. brevispica</i>	0.040	0.059	0.032	0.042	48	26	0.005	0.008	0.036*	F(1,59) = 4.592
<i>A. etbaica</i>	0.008	0.009	0.009	0.010	55	28	0.001	0.002	0.549	F(1,67) = 0.363
<i>Croton dichogamus</i>	0.008	0.011	0.012	0.016	45	24	0.002	0.003	0.647	F(1,57) = 0.213
<i>Grewia bicolor</i>	0.032	0.043	0.031	0.032	44	22	0.005	0.007	0.078	F(1,52) = 3.236

Lower Branches (Dik-dik)	Mean		Stdev		N		SE		P-Values	ANOVA Statistics
	Bush	Open	Bush	Open	Bush	Open	Bush	Open		
<i>A. brevispica</i>	0.037	0.049	0.026	0.042	48	26	0.004	0.008	0.194	F(1,59) = 1.730
<i>A. etbaica</i>	0.008	0.008	0.007	0.008	55	28	0.001	0.001	0.848	F(1,67) = 0.037
<i>Croton dichogamus</i>	0.008	0.014	0.014	0.020	45	24	0.002	0.004	0.156	F(1,57) = 2.072
<i>Grewia bicolor</i>	0.026	0.037	0.024	0.028	44	22	0.004	0.006	0.048*	F(1,52) = 4.086

Upper & lower branches (Impala & Dik-dik)	Mean		Stdev		N		SE		P-Values	ANOVA Statistics
	Bush	Open	Bush	Open	Bush	Open	Bush	Open		
<i>A. brevispica</i>	0.038	0.053	0.024	0.037	48	26	0.004	0.007	0.028*	F(1,59) = 5.093
<i>A. etbaica</i>	0.008	0.008	0.006	0.008	55	28	0.001	0.002	0.817	F(1,67) = 0.054
<i>Croton dichogamus</i>	0.008	0.012	0.012	0.016	45	24	0.002	0.003	0.031*	F(1,57) = 1.060
<i>Grewia bicolor</i>	0.029	0.039	0.024	0.025	44	22	0.004	0.005	0.014*	F(1,52) = 4.351

* Indicate significant difference at $p = 0.05$

Appendix 5. Statistic Summary for Proportion (%) of Biomass Density removed by Impala and Dik-dik.

Upper branches (Impala)	Mean		Stdev		N		SE		P-Values	ANOVA Statistics
	Bush	Open	Bush	Open	Bush	Open	Bush	Open		
<i>A. brevispica</i>	0.555	0.724	0.348	0.295	48	26	0.050	0.058	0.074	F(1,59) = 3.312
<i>A. etbaica</i>	0.388	0.525	0.277	0.307	55	28	0.037	0.058	0.102	F(1,67) = 2.746
<i>Croton dichogamus</i>	0.079	0.094	0.104	0.128	45	24	0.015	0.026	0.978	F(1,57) = 0.001
<i>Grewia bicolor</i>	0.529	0.744	0.333	0.305	44	22	0.050	0.065	0.014*	F(1,52) = 6.415
Lower Branches (Dik-dik)	Mean		Stdev		N		SE		P-Values	ANOVA Statistics
	Bush	Open	Bush	Open	Bush	Open	Bush	Open		
<i>A. brevispica</i>	0.542	0.595	0.362	0.331	48	26	0.052	0.065	0.330	F(1,59) = 0.966
<i>A. etbaica</i>	0.586	0.571	0.288	0.251	55	28	0.039	0.047	0.850	F(1,67) = 0.036
<i>Croton dichogamus</i>	0.098	0.139	0.164	0.179	45	24	0.024	0.037	0.196	F(1,57) = 1.714
<i>Grewia bicolor</i>	0.554	0.734	0.351	0.299	44	22	0.053	0.064	0.069	F(1,52) = 3.447
Upper & lower branches (Impala & Dik-dik)	Mean		Stdev		N		SE		P-Values	ANOVA Statistics
	Bush	Open	Bush	Open	Bush	Open	Bush	Open		
<i>A. brevispica</i>	0.558	0.679	0.322	0.259	48	26	0.046	0.051	0.043*	F(1,59) = 4.268
<i>A. etbaica</i>	0.498	0.561	0.234	0.244	55	28	0.032	0.046	0.298	F(1,67) = 1.102
<i>Croton dichogamus</i>	0.089	0.107	0.121	0.129	45	24	0.018	0.026	0.392	F(1,57) = 0.744
<i>Grewia bicolor</i>	0.539	0.739	0.303	0.285	44	22	0.046	0.061	0.032*	F(1,52) = 4.871

* Indicate significant difference at $p = 0.05$

Appendix 6. Summary Statistics for Biomass Density (g/cm) of Leaves Remaining After Exposure to Impala and Dik-Dik

Upper branches (Impala)	Mean		Stdev		N		SE		P-Values	ANOVA Statistics
	Bush	Open	Bush	Open	Bush	Open	Bush	Open		
<i>A. brevispica</i>	0.034	0.022	0.032	0.026	48	26	0.005	0.005	0.033*	F(1,59) = 4.768
<i>A. etbaica</i>	0.010	0.007	0.008	0.008	55	28	0.001	0.002	0.014*	F(1,67) = 6.404
<i>Croton dichogamus</i>	0.097	0.095	0.039	0.033	45	24	0.006	0.007	0.939	F(1,57) = 0.006
<i>Grewia bicolor</i>	0.025	0.013	0.019	0.016	44	22	0.003	0.004	0.005*	F(1,52) = 8.492
Lower Branches (Dik-dik)										
Lower Branches (Dik-dik)	Mean		Stdev		N		SE		P-Values	ANOVA Statistics
	Bush	Open	Bush	Open	Bush	Open	Bush	Open		
<i>A. brevispica</i>	0.034	0.035	0.034	0.040	48	26	0.005	0.008	0.900	F(1,59) = 0.014
<i>A. etbaica</i>	0.005	0.006	0.005	0.006	55	28	0.001	0.001	0.711	F(1,67) = 0.138
<i>Croton dichogamus</i>	0.090	0.088	0.042	0.046	45	24	0.006	0.009	0.753	F(1,57) = 0.100
<i>Grewia bicolor</i>	0.020	0.013	0.020	0.017	44	22	0.003	0.004	0.114	F(1,52) = 2.578
Upper & lower branches (Impala & Dik-dik)										
Upper & lower branches (Impala & Dik-dik)	Mean		Stdev		N		SE		P-Values	ANOVA Statistics
	Bush	Open	Bush	Open	Bush	Open	Bush	Open		
<i>A. brevispica</i>	0.033	0.026	0.028	0.031	48	26	0.004	0.006	0.204	F(1,59) = 1.651
<i>A. etbaica</i>	0.007	0.006	0.005	0.007	55	28	0.001	0.001	0.174	F(1,67) = 1.890
<i>Croton dichogamus</i>	0.091	0.091	0.029	0.031	45	24	0.004	0.006	0.574	F(1,57) = 0.319
<i>Grewia bicolor</i>	0.022	0.012	0.017	0.014	44	22	0.003	0.003	0.013*	F(1,52) = 6.626

* Indicate significant difference at $p = 0.05$

Appendix 7. Summary Statistics for the Proportion (%) of Biomass Density of Leaves Remaining after Exposure to Impala and Dik-dik

Upper branches (Impala)	Mean		Stdev		N		SE		P-Values	ANOVA Statistics
	Bush	Open	Bush	Open	Bush	Open	Bush	Open		
<i>A. brevispica</i>	0.445	0.276	0.348	0.295	48	26	0.050	0.058	0.051	F(1,59) = 3.961
<i>A. etbaica</i>	0.612	0.475	0.277	0.307	55	28	0.037	0.058	0.048	F(1,67) = 4.057
<i>Croton dichogamus</i>	0.921	0.906	0.104	0.128	45	24	0.015	0.026	0.505	F(1,57) = 0.451
<i>Grewia bicolor</i>	0.471	0.256	0.333	0.305	44	22	0.050	0.065	0.001	F(1,52) = 11.455

Lower Branches (Dik-dik)	Mean		Stdev		N		SE		P-Values	ANOVA Statistics
	Bush	Open	Bush	Open	Bush	Open	Bush	Open		
<i>A. brevispica</i>	0.458	0.405	0.362	0.331	48	26	0.052	0.065	0.789	F(1,59) = 0.072
<i>A. etbaica</i>	0.414	0.429	0.288	0.251	55	28	0.039	0.047	0.391	F(1,67) = 0.744
<i>Croton dichogamus</i>	0.902	0.861	0.164	0.179	45	24	0.024	0.037	0.530	F(1,57) = 0.399
<i>Grewia bicolor</i>	0.446	0.266	0.351	0.299	44	22	0.053	0.064	0.110	F(1,52) = 2.643

Upper & lower branches (Impala & Dik-dik)	Mean		Stdev		N		SE		P-Values	ANOVA Statistics
	Bush	Open	Bush	Open	Bush	Open	Bush	Open		
<i>A. brevispica</i>	0.4424	0.3206	0.3218	0.2587	48	26	0.046	0.051	0.232	F(1,59) = 1.458
<i>A. etbaica</i>	0.5019	0.4393	0.2343	0.2444	55	28	0.032	0.046	0.165	F(1,67) = 1.969
<i>Croton dichogamus</i>	0.9115	0.8926	0.1211	0.1293	45	24	0.018	0.026	0.574	F(1,52) = 0.319
<i>Grewia bicolor</i>	0.4606	0.2614	0.3031	0.2855	44	22	0.046	0.061	0.003	F(1,52) = 9.542

* Indicate significant difference at $p = 0.05$