THE EFFECTS OF HERBIVORY ON INTERACTIONS OF POLLINATORS AND

FLOWERS IN *ACACIA* SPP. (FABACEAE, MIMOSOIDEAE) IN LAIKIPIA

DISTRICT OF KENYA.

By

MARK OTIENO [B. Ed. (Science) Hons. K.U.]

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENT

FOR THE DEGREE OF MASTER OF SCIENCE (ANIMAL ECOLOGY) OF

KENYATTA UNIVERSITY.

MAY 2005

DECLARATION

This thesis is my original work and has not been presented for a degree in any other university or any other award.

Signature……………………… Date………………………………

Mark Otieno

We confirm that the work reported in this thesis was carried out by the candidate under our supervision.

Signature……………………… Date……………………..

Dr. Callistus K.P.O. Ogol

Department of Biological Sciences, Kenyatta University.

Signature……………………… Date……………………….

Prof. Pat Willmer
School of Biology, University of St. Andrews.

DEDICATION

To the Almighty God for providing all I needed to achieve this work and to my family

for their longest serving friendship.

ACKNOWLEDGEMENTS

ABSTRACT

Acacia trees are among the most dominant tree species found in semi arid ecosystems with a vast geographical distribution throughout the savanna habitats. The trees are leguminous and have remarkable ability to fix nitrogen in the soil, thereby, improving fertility. About all parts of an *Acacia* tree are edible to different types of animals and their leaves provide the only greenery in the dry season, so are bound to be eaten. As such, they support enormous pyramids of biomass in complex food chains with super predators at the apex. Economically, they are used as basic sources of fruits, firewood, medicine and secondary products for daily human livelihoods. Owing to their importance, a lot of studies have focused on their growth ecology. Herbivory and reproduction are among the most studied aspects of *Acacia*. However, the interactive link between these two aspects and their effect on the growth success of Acacias is poorly understood. Understanding the link between herbivory and pollination, would not only provide useful information on the interaction of plants and diversity of visitors but also information on the floral morphometry and rewards to pollinators. The general objective of this study was to determine the effects of herbivory on interactions between pollinators and flowers in *Acacia* spp. The study was conducted at the Mpala Research Centre in Laikipia District of Kenya (0°17'N, 36°53'E) on one herbivore excluded plot (70m×50m) and in the open grazed areas adjacent to the exclusion plot. *Acacia* trees for investigation were randomly selected. Data were recorded on floral morphometric measurements and dehiscence in different browsing levels and simulated herbivory plots. The number and type of visitors to the flowers was also recorded besides determining the species diversity of wild flora within the study site. ANOVA was used to analyze variation in different flower attributes, SNK was used to separate means with significant differences. Generally, unbrowsed trees produced significantly (P<0.05) more flowers, florets, anthers and larger floral diameters than naturally and heavily browsed *Acacia* trees. Similarly, unbrowsed trees attracted more pollinators especially bees than naturally browsed trees. An earlier pollinator peak activity was recorded on unbrowsed trees than browsed trees. A significant shift of inflorescence dehiscence time occurred between unbrowsed and naturally browsed trees of *A. nilotica*, (KS=0.34, P<0.01), *A. brevispica* (KS=0.34, P<0.01) and *A. etbaica* (KS=0.33, P<0.01) across the day. The unbroswed trees attracted significantly more pollinators than naturally browsed trees probably because the unbrowsed trees had larger flowers thereby becoming more visible to pollinators from a distance than those of browsed trees. The delayed floral dehiscence of naturally browsed trees could have been caused by modification of the microclimate around the flowers making them open later in the day than unbrowsed trees. This study has shown that *A. nilotica* and *A. brevispica* vary their floral resources greatly when browsed, whereas *A. etbaica* tends to show compensatory floral growth. More studies therefore, need to be done on their reproductive success.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

LIST OF APPENDICES

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

1.1 INTRODUCTION

Trees are essential in the functioning of savanna ecosystems as they increase water and nutrient infiltration and also enhance nutrient cycling in the soil by their complex root structure and control soil erosion (Shaw e*t al.,* 2002). In addition to this ecological role, leguminous trees like those of genus *Acacia* (Fabaceae, Mimosoideae) have the ability to fix atmospheric nitrogen to the soil, increasing fertility (Belsky, 1994; Shaw *et al.,* 2002).

Acacias are among the most dominant woody plants in many tropical and subtropical semi arid habitats across the world (Ross, 1981; Coe and Coe, 1987; Coe and Beentje, 1991; Rohner and Ward, 1999; Or and Ward, 2003; Stone *et al.,* 2003). The trees are of great economic value to human societies as they are used as sources of timber wood. The trees are also used as wood fuel as they are reknown for their excellent combustion properties and produce good charcoal; they also often yield useful fruits and secondary plant compounds (Turnbull, 1987; Beentje, 1994; Midgely and Turnbull, 2003). In other cases, the trees are used as animal fodder as the pods and leaves contain 8% digestible protein (12.4% crude protein), 7.2 MJ/kg energy, and are rich in minerals (Le Houerou, 1980). Ecologically, acacias support a large animal biomass combining a great diversity of both vertebrate and invertebrate herbivores (Krüger and Mc Gavin, 1998).

The genus *Acacia* comprises a heterogeneous assembly of over 1000 species most of which are trees (Brain, 1987). The largest number of *Acacia* spp. is found in Australasia, and a few of these Australasian species have been introduced in East Asia and Africa, where many have become serious weeds (Milton and Moll, 1982; Morgan *et al.,* 2002; Paynter *et al.,* 2003; Stone *et al.,* 2003) and where they may compete with the indigenous species. In Kenya, there are more than 100 listed *Acacia* species (Coe and Beentje, 1991).

Herbivory and pollination are among the most studied aspects of *Acacia* trees (Palmer and Young, 2000). The species in this genus have been used as models for animal- plant interaction research, particularly ant-plant mutualisms, for many decades (Regino, 2000; Raju and Rao, 2002). Although most of the studies done on acacias have focused, to large extent, on aspects of herbivory and pollination ecology treated independently, the two have a close association and cannot be separated in nature.

1.2   LITERATURE REVIEW

1.2.1   PLANT HERBIVORY

Herbivores can have serious negative impacts on the growth, reproduction, and the population size of plants (e.g. Howe and Westley, 1988; Rosenthal and Berenbaum, 1992; Marquis and Whelan, 1994). Plants possess numerous physical and chemical traits that protect them from herbivore attack, including trichomes (Levin, 1973), toughness (Grubb, 1986), and a diverse arsenal of deterrent secondary metabolites (Rosenthal and Janzen, 1979; Hay and Fenical, 1988; Rosenthal and Berenbaum, 1992). In addition to defensive plant traits, plants can also achieve reduced herbivory

via symbiotic relationships with other plants (Hay, 1986), fungi (Clay, 1988), or animals (Janzen, 1966).

Gaad *et al.* (2001) highlight plant responses to herbivore attack through tolerance, compensation or induced defense. Tolerance is a plant's ability to withstand and survive damage. Compensation is increased plant growth after loss of tissue to herbivores (Strauss and Agrawal, 1999). Induced responses to herbivory are called 'induced defense' when they are known to decrease rates of herbivory (Karban and Baldwin, 1997). A potential specific response to herbivory is therefore, for the plant to increase its defensive capabilities. This induced defense can be adaptive in situations where herbivory is variable, and where current herbivory is a good predictor of future herbivory (Karban and Baldwin, 1997; Agrawal, 1998; Gaad *et al.,* 2001). McNaughton (1983) reports that responses to herbivory are complex and may depend on the timing of herbivory, the type and extent of herbivory, the availability of resources in the environment to support regrowth, and the grazing or browsing history of the plant.

1.2.1.1 DIFFERENT SCALE OF EFFECTS OF HERBIVORY BY VERTEBRATES AND INVERTEBRATES

Damage to a plant by herbivores is scored as major when it is associated with the removal of virtually all photosynthetic tissue severe enough to lead to death. Such major damage can clearly affect the composition of the tree flora in a given area, especially via tree recruitment. Many studies have been done on effects of different herbivores on tree recruitment (Ostfeld and Canham, 1993; Hulme, 1996; Ostfeld *et al.,* 1997). Rodents have been documented as the major primary herbivores affecting

temperate woodland and forest tree recruitment (Shaw *et al.,* 2002). However, in tropical savannas it has been reported that ungulate herbivores are the key filters on tree regeneration and recruitment (Dublin, 1995; Sinclair, 1995; Shaw *et al*., 2002). At the seedling stages of a tree, though, Shaw *et al.* (2002) showed that invertebrates account for the majority of serious herbivores, being associated with 90% of major damage; thus mammalian herbivores have much less impact on regeneration but have a major impact on adult trees (Shaw *et al.,* 2002).

Recent studies indicate that different guilds of herbivores inflict different scales of damage to plants. The work by Shaw *et al.* (2002) provides a comprehensive understanding of these scales of effects. When trees are at seedling and sapling stages of their growth cycle, exclusion of mammalian herbivores generally leads to maximum damage being inflicted to the trees by a diverse assembly of different invertebrate herbivore communities and this could be linked to an increased biomass of herbaceous vegetation (Shaw *et al.,* 2002). The few trees that escape this invertebrate-derived damage provide the browse material for larger animals, especially ungulates, which become the most important herbivores and can inflict maximum damage (Crawley, 1983; Shaw *et al.*, 2002). However, the different scales of effects of herbivory by vertebrates and invertebrates specifically on *Acacia* species are poorly understood, and limited literature exists on this subject.

1.2.1.2 *ACACIA* HERBIVORY

Acacia species suffer considerable herbivory in nature (Gaad *et al.,* 2001*)*. They support very complex food webs and large biomass, and many herbivores prefer them as their food sources. *Acacia* trees show great compensatory growth for some forms

of herbivory, presumably because the trees are so predictably browsed by herbivores (Gaad *et al.,* 2001).

Previous surveys have shown that when herbivores are excluded from *Acacia* trees, shoot and leaf herbivory are effectively reduced (Young and Okello, 1998; Young *et al*., 1998). Gaad *et al.* (2001) report that such exclusion of herbivores is associated with about 60% greater shoot growth on trees protected from browsers. Research has also shown that there may be at least some costs of herbivory that are not fully recoverable by shoot regrowth, either differences in shoot mortality or systemic responses of trees to herbivory (Gaad *et al.,* 2001). Growth effects following herbivory are fairly similar regardless of the type of herbivore involved. It is however not known if such regrowth following exclusion of browsers is also associated with an increase in flower production and rewards.

1.2.1.3 *ACACIA* **HERBIVORES**

There is a diverse array of herbivores reported to browse on *Acacia* in tropical ecosystems (Miller, 1995). The major herbivores can be grouped into two categories: vertebrates (mostly mammals) and invertebrates (mostly insects).

Large mammal herbivores include: elephants (*Loxodonta africana*), giraffes (*Giraffa camelopardalis*), cape buffalos (*Syncerus caffer*), elands (*Taurotragus oryx*), Grevy's zebras (*Equus grevyi*), Burchell's zebras (*Equus burchelli*), Beisa oryx (*Oryx beisa*), Jackson's hartebeests (*Alcelaphus buselaphus jacksoni*), Grant's gazelles (*Gazella granti*), steinbucks (*Raphicerus campestris*) and domestic cattle (Young *et al*., 1998). These large vertebrates graze on and damage the trees in different ways. Giraffes, for example, strip the branches of their leaves and nip young shoots (Pellew, 1983;

Milewski et al., 1991; Young and Isbell, 1991), while elephants may break off whole branches.

Small mammal herbivores are mainly rodents, and include *Saccostomus mearnsi*, *Arvicanthis nairobae*, *Mus minutoides*, *Mastomys natalensis*, *Dendromus melanotis* and *Crocidura* spp. (Keesing, 1998). There are many types of invertebrate herbivores reported, most of which are insects, especially beetles (Coleoptera), plant bugs (Hemiptera) and butterfly and moth caterpillars (Lepidoptera) (Gaad *et al.,* 2001).

1.2.2   PLANT POLLINATION

Pollination is a process involving flowers [the pollen source (anthers) and receiver (stigmas)] and a pollination vector (an agent carrying pollen to the stigma). Pollen itself may be the primary food reward, while nectar is a secondary reward and is commonly produced as "bribe". In addition, floral coloration patterns such as streaks, spots, or patches guide the pollinator to the nectar (Bawa and Hadley, 1990). As the pollinator takes a 'drink', it brushes against the sex organs of the flower thereby pollinating it (Grant, 1984). Bees are the most important pollinators for many plants and a great deal of research has focused on their foraging behavior and pollen utilization, which can only be briefly reviewed here.

1.2.2.1 FLORAL REWARDS AND ATTRACTANTS

Within any limits imposed by ambient abiotic conditions, the timings of floral resource availabilities in a particular flower species have obvious consequences for the pollinators that rely on them. Several resources are relevant:

i. POLLEN

Pollen is a good food source for many pollinators and is crucial for cell provisioning in almost all bees. The timing of pollen release (dehiscence) therefore, has particular significance for female bees. Some pollen may also be ingested, especially by younger foragers, to provide the protein needed for egg maturation (Michener, 2000). Bees can routinely carry 20-25% of their body weight as a pollen load, and this figure may exceed 35-40% on occasion for larger bees (Michener, 2000).

ii. NECTAR

Nectar is basically a solution of sugars, which is secreted from the plant into a particular receptacle termed a nectary. These are usually within the flowers, so visitors go to the flowers for the food and may thereby contact pollen (Faegri & Van der Pijl 1979).

iii. OILS AND RESINS

A small proportion of plants offer oils as alternative rewards, used by some pollinators (especially solitary bees) as larval food. Furthermore, oils and resins are used for nest building in some species e.g. *Dalechampia* sp. (Armbruster, 1984), but they are also gathered more generally by bees, including *Apis*, for incorporation in the nest, perhaps because they often have antibacterial and antifungal properties (classic examples are gum Arabic resins from certain *Acacia*, and myrrh and frankincense from *Commiphora* species in Africa). Where these are carried on the scopae they preclude simultaneous pollen collection (Michener, 2000).

iv.   SCENTS

Some orchids produce aromatic scents that are gathered by some pollinators and perhaps used as pheromone components. This has been recorded in male euglossine bees (Kimsey, 1980; Dressler, 1982). It has been shown that scents are collected and accumulated throughout adult life (and sometimes even stolen from dead males) to signal longevity and suitability as a mate (Roubik, 1998; Eltz *et al.,* 1999).

Normally, taking on nectar or pollen loads will entail visits to many tens or even hundreds of flowers within a foraging trip, the number being generally less for pollen than for nectar, and roughly related to the size and specificity of the pollinator. Solitary bees may make specific trips for single resources but often take both resources on any one trip; social bees more commonly forage for just one resource at a time.

1.2.2.2 *Acacia* POLLINATION AND FLORAL REWARDS

Kenrick (2003) reviews in detail the reproductive biology of *Acacia* flowering. The flowers of these trees are carried in heads called "inflorescences" which range in shape from spherical (globose) to elongate (spicate) depending on the species (Stone *et al.,* 2003). The number of flowers per inflorescence greatly varies both intraspecifically and extraspecifically as does the number of stamens per flower, as reported by Tybirk (1989), Sedgely *et al.* (1992) and Kenrick (2003). Many acacias produce flowers containing only stamens, often over the entire inflorescence (Stone *et al.,* 2003). This flowering behaviour may be important in recruiting a limited pool of pollinators by provision of abundant pollen reward. There are two main types of floral rewards available to *Acacia* pollinators: pollen and nectar.

a) *ACACIA* POLLEN

Acacia is unusual in that pollen grains are not separate but are amalgamated into "polyads". A great variation exists in the size and number of pollen grains contained in each polyad in *Acacia* species (Kenrick and Knox, 1982; Kenrick, 2003; Stone *et al*., 2003) though 4, 8 and 16 are common. It is reported that pollinators harvest polyads as units, which suggests that their size and nutritional value may be a factor in the choice of forage plant (Bernhardt and Walker, 1984). The amount of pollen presented by the flower on each polyad would partly determine the number of pollinators that are attracted to the flower.

Acacia pollen may also be involved in long-range attraction of visitors, both as a visual and an olfactory cue, as well as serving a reproductive role and acting as a food source for pollinators. The pollen is the main source of colour in most *Acacia* flowers, and is held superficially, on the outer surface of the inflorescence. Furthermore, some of the tissues producing floral scent are located inside the anthers and associated structures (Tybirk, 1993; Kenrick, 2003). Thus all *Acacia* flowers offer strong attractant signals, but a purely staminate flower represents a particularly powerful visual and olfactory attractant to pollinators. This kind of attraction may be important if co-flowering acacias compete for pollinators (Bernhardt and Walker, 1984; Stone *et al.,* 2003).

b) *ACACIA* FLORAL NECTAR

Acacias do not commonly secrete floral nectar. However, some species of *Acacia* do secrete small volumes of nectar. These include: *A. zanzibarica* and *A. tortilis*, *A. brevispica*, *A. mellifera* and *A. senegal* (Stone *et al.,* 1998; Tandon *et al.,* 2001; Stone

et al., 2003). It is reported that the quantity and quality of nectar varies a lot among species of *Acacia*. The time of day is also a critical factor on the availability of nectar. The activity of some kinds of pollinators (especially bees and butterflies) would be expected to positively correlate with nectar availability. However availability is in itself a complex issue; it depends of course upon the timing of secretion by the plant, but is strongly modified by continuous harvesting and by evaporation, both of which can cause a reduction of nectar quantity, and hence a reduction in the number of pollinators to the flowers (Stone *et al.,* 2003).

1.2.2.3   FLOWER LONGEVITY

There is a great variation in the flower longevity among species of *Acacia* (Stone *et al.,* 2003). In most, including nearly all the African species, the flowers open and dehisce on a single day (Tybirk, 1989; Stone *et al.,* 1996; Tandon *et al.,* 2001; Stone *et al.,* 2003), and are senescent on day 2.

Species with globose flower inflorescences have been reported to flower synchronously over the whole inflorescence in African species (for example, *A. drepanolobium, A. etbaica, A. brevispica, A. seyal, A. zanzibarica, A. tortilis* and *A. reficiens*; Tybirk, 1989; Stone *et al.,* 1998). In species with spicate inflorescences, opening may occur on the same day over the whole flower head as in *A. hindsii* (Raine, 2001) or may be staggered such that groups of neighbouring flowers open on the same day, with those basal flowers in the inflorescence opening first as in *A. bussei, A. senegal,* and *A. thomasii* (Tybirk, 1993; Stone *et al.,* 1998). In the absence of rain, the whole inflorescence in such species flowers in 3 days or less (Tybirk, 1993; Stone *et al.,* 1998).

1.2.2.4 TIMING OF REWARD PRESENTATION

Studies have shown that time of pollen release in *Acacia* ranges from dawn to mid-afternoon (Stone *et al.,* 1998). Anther dehiscence in many *Acacia* species is precisely structured in time, with a sharp peak of anther availability usually in the morning. However in species such as *A. zanzibarica, A. senegal, A. drepanolobium* and *A. nilotica,* the time of peak pollen presentation is more protracted (Stone *et al.,* 1996). *Acacia nilotica* flowers, for example, usually begin to open during the night, and anthesis occurs before dawn with full anther dehiscence reached around 10h00. In *A. zanzibarica* and *A. drepanolobium,* flowers begin opening around dawn and are not fully dehisced until around 10h00 and 12h00 respectively (Stone, *et al.,* 1996*;* Stone *et al.,* 1998). In these species, the exact timing of dehiscence can also be quite variable, depending on both location and ambient conditions (Stone *et al.,* 1996).

The difference in pollen presentation between species is very crucial, especially in different species that grow together, because it can reduce competition for pollinators (Levin and Anderson, 1970; Ollerton and Lack, 1992; Stone *et al.,* 1998). First of all, this difference could result in temporal partitioning of pollinator behaviour to avoid competition for pollinator visits; and secondly, because many pollinators remove pollen from their bodies at regular intervals (Gilbert, 1981; Roubik, 1989, Stone *et al.,* 1998), temporal partitioning of their activity will result in pollinators carrying predominantly one type of pollen at any one time, so reducing interspecific pollen transfer (Stone *et al.,* 1998).

Dehiscence is associated with the release of strong, species-characteristic scents that may provide a synchronizing cue announcing availability of fresh standing crop in

each species (Willmer and Stone, 1997). Flower visitors such as bees, both solitary and social, are known to be sensitive to floral reward availability especially pollen (Frankie *et al.,* 1983; Buchman and Cane, 1989, Stone *et al.,* 1998), and switching of foraging between *Acacia* species through the day is to be expected. In addition, those species that are nectar-producing will receive a substantial proportion of visiting insects that are absent from the guilds of pollen-only acacias (Armbruster and Herzig, 1984; Rathcke, 1988; Stone *et al.,* 1998).

1.2.2.5   *ACACIA* POLLINATORS

Bees form a majority of *Acacia* pollinators. A few examples of larger pollinating bees include *Apis mellifera*, *Xylocopa* and *Amegilla* spp., while smaller species include *Plebeina*, *Braunsapis* and various halictids. Other groups of pollinators include flies, butterflies, beetles, wasps, ants, birds and bats (Stone *et al.,* 2003), with the balance between these groups varying for different species of *Acacia*.

1.2.3   INTERACTIONS OF HERBIVORY AND POLLINATION

Research programs on plant-animal interactions have generally produced studies focusing on just one of the key kinds of interaction (i.e. herbivory, pollination or seed predation/dispersal), which lead to oversimplification of the real ecological interactions that go on in nature. In reality these different sets of animal-plant interactions can combine in several different fashions, to exert an intricate influence on plants (Heithaus *et al.,* 1982; Schemske and Horvitz, 1988; Herrera, 1989, 1993; Cunningham, 1995; Herrera, 2000).

Study of the effect of foliar herbivory on plant reproductive success has traditionally focused on seed set or fruit production, revealing that the decrease in resources that occurs due to foliar herbivory can reduce the number of seeds and fruits produced by flowering plants. For example, Rausher and Simms (1989) found that beetle herbivory of *Ipomoea purpurea* reduced seed production by 20%. Marquis (1992) also found that a 10% loss of leaf area in *Piper arieianum* resulted in a significant decrease in both leaf growth and seed production. However, since the 1970's it has often been suggested that reduction in resources through herbivory, especially by insects, may affect the energy available to invest in the reproductive characters (i.e. the floral traits) of the host plant, so influencing pollinator visitation and providing an indirect route to altered seed set. It is well known that natural variation in pollen, nectar, and flower size and number affects the attractiveness of plants to pollinators. However, to date, very few studies have directly tested the link between foliar herbivory and pollinator attraction; and those studies, which are available, have mainly concentrated on just 2 or 3 species of annual plants.

The first study investigating the effect of foliar herbivory on reproductive fitness of male plant characters was that of Quesada *et al.* (1995), which investigated the effect of leaf damage on pollen production and competitive ability in wild zucchini (*Curcurbita texana*), by removing 15% of the leaf area with a hole punch, simulating natural beetle herbivory. Their results revealed that pollen production per flower was significantly reduced by herbivore damage, and that flower production was decreased, adding to the total decrease in pollen per plant. By placing pollen from undamaged and damaged plants on the same stigma, the study further showed that pollen from damaged plants was also competitively inferior. Mutikainen and Delph (1996)

followed up this study by simulating herbivory on *Lobelia siphilitica* by removing the bottom third of all leaves from each plant, and concluded that pollen tubes from control plants grew significantly faster than those from damaged plants.

The studies discussed so far are recognized as comprising most of the work carried out to date on the effect of herbivory on pollen and flower production, suggesting how recent the study in this area is, and how poor our knowledge of the effects of herbivory on reproductive success of plants remains. However, from the findings of these studies, it is clear that they support the hypothesis that herbivory can affect the number of pollen grains produced, the size and competitive ability of these grains. This would suggest that plants under herbivore attack are less likely to sire seed successfully than their undamaged counterparts, i.e. their male function will be reduced. This might in turn result in natural selection for plants that are less susceptible to herbivore attack. It also shows that maternal fitness (which is more commonly measured) does not accurately reflect total plant fitness in at least some plant species.

Pollen size, amount and competitive ability, and resultant paternal success are in turn likely to be related to and/or influenced by corolla size, which is an important visual cue for most pollinators. It has been shown that, all other things being equal, the distance at which a bumblebee is attracted visually to a flower is directly proportional to the flower diameter. Small flowers are often organized in inflorescences, increasing the display size, which can increase attractiveness, as can plant density (Murawski, 1987). Studies testing the effect of flower size and number on pollinator preference include that of Galen (1989), who showed that bumblebees preferred alpine sky pilot

(*Polemonium viscosum*) flowers with larger corolla diameters; and Conner and Rush (1996), who found that larger corolla sizes and increased flower numbers per plant in wild radish (*Raphanus raphanistrum*) were preferred by syrphid flies.

The effects of herbivory on corolla size have therefore, recently been considered. Frazee and Marquis (1994) found that simulated herbivory by clipping the leaves of *Chamaecrista fasciculata* did not affect corolla size. In contrast, Strauss *et al.* (1996) found that *Raphanus raphanistrum* damaged by *Pieris rapae* larvae produced significantly shorter and thinner petals than the control plants. A repeat of the study by Lehtila and Strauss (1999) upheld the original result of a decrease in petal size. Strauss (1997) damaged wild tobacco (*Nicotiana attenuata*) by perforating the leaf surface, therefore, eliminating any effect of leaf removal. She found that damaged plants again exhibited a significantly smaller corolla size.

 The shape of flowers can also influence the type of pollinator that is attracted. Bumblebees, for instance, prefer bilaterally symmetrical flowers, whereas honeybees favor radially symmetrical flowers (Davenport, 1982). Other flower traits affecting visitation include the 'edginess' of the corolla – the circumference to surface area ratio. It has been found that butterflies, honeybees and bumblebees all prefer a more 'edgy' flower (Barth, 1985). Again, these traits could be affected by herbivore leaf damage, though this has not been explored. However, Lehtila and Strauss (1997) did take matters somewhat further by showing that leaf damage by herbivores on wild radish (*Raphanus raphanistrum*) did affect the floral attractiveness to pollinators, thus reducing the reproductive fitness of this plant.

The few studies done on interactions of herbivory and pollination of plants have indicated that foliar herbivory may cause a reduction in the amount, size and competitive ability of pollen grains, alterations in flower size or number, delays to flowering time, and reduced attractiveness to some pollinators. Strauss *et al.* (1996) go further and suggest that foliar herbivory may actually change the pollinator species composition, for example if only certain male traits (e.g. petal size and not flower number) are affected. Changes in pollinator behavior or species composition as a result of herbivory could have profound effects on the population structure of plants. For instance, some species may be better pollen dispersers compared to other species. If species of pollinators promoting out-crossing were less attracted to damaged plants, this could increase the amount of inbreeding within damaged plants. The preferences of pollinators may also act as selective pressures that shape how plants allocate resources. For instance, a plant mainly pollinated by a solitary bee species may be selected to conserve flower number over petal size when damaged by herbivores, as this is the trait used to attract its main pollinator. Plants with a diversity of pollinators may also have more flexibility in their response to herbivory, whereas plants with a single pollinator may have to conserve the floral traits which this species uses as an attractant (Strauss *et al.,* 1996).

However, all the studies to date have concentrated on annual plants and they have mainly been done in laboratories and greenhouses. There is need for work on large perennial plants and trees, in natural surroundings, and for work relevant to large vertebrate herbivores, rather than just insects. Furthermore, work of this nature has not as yet been done in any *Acacia* species, which are major primary producers and

sustain the bulk of biomass in semi arid habitats across the globe and of great economic value to local populations.

1.3 RATIONALE

Acacia trees are well distributed throughout the savanna habitats, particularly the semi arid areas where humans use them as basic sources of fruits, firewood and secondary products for their daily livelihoods. The trees perform critical ecological roles forming food sources for many herbivores therefore, supporting enormous biomass in complex food chains. In addition, they facilitate the fixation of free atmospheric nitrogen into the soil and also maintain soil structure through their dense network of roots. Understanding the link between herbivory and pollination in *Acacia* would not only provide useful information on the interaction of plants and their diverse visitors, and on the floral morphometry and rewards to pollinators, but also information relevant to conservation of *Acacia* communities and populations. It is important to understand not only the immediate damage caused by herbivores, but also the 'knock-on' effects of herbivory on *Acacia* floral attributes and pollinator diversity, because these characters determine the trees' reproduction and eventual recruitment (and may also affect pollinator diversity for other plants in the community). In short, the variation of flower production and floral resources due to natural grazing at different levels provides a key link between pollinators and herbivores, and a crucial component of ecosystem functioning.

1.4   STUDY HYPOTHESES

1) Herbivory has no effect on flower morphometry and abundance in *Acacia.*

2) Herbivory does not affect floral rewards availability to pollinators.

3) Herbivory has no effect on *Acacia* pollinator diversity and abundance.

4) Herbivory has no effect on the interaction between pollinators and flowers of different *Acacia* species.

1.5   OBJECTIVES

1.5.1   GENERAL OBJECTIVE

To determine the effects of herbivory on interactions between pollinators and flowers in *Acacia* spp. in Laikipia District of Kenya.

1.5.2 SPECIFIC OBJECTIVES

1. To determine the effect of herbivory on flower morphometry and flower abundance in *Acacia* spp.

2. To establish the effect of herbivory on floral rewards availability to pollinators.

3. To establish the effect of herbivory on *Acacia* pollinator diversity and abundance.

4. To assess the effect of herbivory on the interaction between pollinators and flowers of different *Acacia* species.

CHAPTER 2

MATERIALS AND METHODS

2.1   DESCRIPTION OF STUDY AREA

The study was carried out at the Mpala Research Centre (M.R.C.) located in Laikipia

District, Central Kenya (0°17'N, 36°53'E). The property (20,000 ha/48,000 acres) is

situated northwest of Mt. Kenya, 50km north of the Equator, and 50km from

Nanyuki town (Fig. 1).
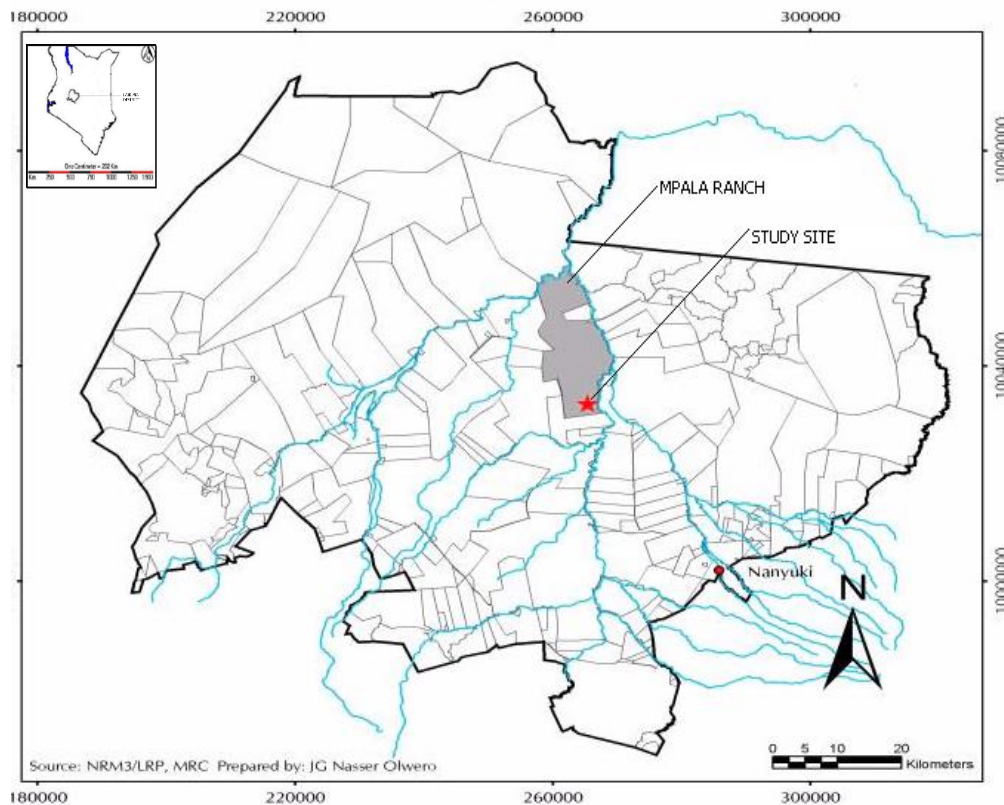
Figure 1: Map of Laikipia District (inset: Kenya) showing study site

Warm days and cool nights predominate, with low humidity in the driest season

(January-April), and moderate humidity at other times. The rainfall is weakly

trimodal, with peaks in April-May, July-August, and October-November, and a distinct dry season in January-February. There is considerable year-to-year variation in total rainfall and in the seasonal distribution of rainfall. The property spans an altitudinal and climatic gradient that is higher, wetter and cooler in the southwest (1850 m a.s.l., 530 mm annual rainfall), and lower, drier and hotter in the northeast (1550 m a.s.l., 400 mm annual rainfall) (http://www.mpalafoundation.org).

The northern two-thirds of Mpala is underlain by dissected Archean terrain with thin dark red sandy loams (latosols). The southwestern one-third of the property is characterized by a 100 m high phonolite lava flow. Soils developed on the flow consist of a catena of black clay vertisols with impeded drainage, with brown calcareous loams (chestnut soils) on the higher elevations and steeper slopes. Scattered throughout this terrain are granitic inselbergs or kopjies, with the largest, 'Mukenya' (1846 m a.s.l.), at the center. Fifteen dams have been constructed on Mpala, and there are more than 250 km of internal roads (http://www.mpalafoundation.org)

An estimated 800 plant species occur in Mpala. The vegetation is characteristic of semi-arid African savanna, predominantly grassy savanna bushland, with patches of woodland and open grassland. Dominant trees include species in the genera *Acacia* (Mimosaceae), *Euphorbia* (Euphorbiaceae), *Balanites* (Balanitaceae), and *Boscia* (Capparaceae) (http://www.mpalafoundation.org).

More than 2,000 cattle, camels and sheep are ranched in Mpala, but the region also hosts an intact savanna mammal community, including Kenya's second largest

elephant population. Currently 85 mammal species and at least 300 bird species can be found in Mpala. Elephant, eland, plains zebra, oryx and giraffe are seasonally abundant, depending on rainfall and forage availability. Waterbuck, impala, Grant's gazelle, Jackson's hartebeest and bushbuck are resident. Lions, leopards, cheetahs, spotted hyenas, black-backed jackals, aardwolfs and bat-eared foxes are also seen regularly (http:// www.mpalafoundation.org).

Profound changes in patterns of biodiversity occur along altitudinal and climatic gradients that extend from the Mt. Kenya and the Aberdare Highlands in the south (3500m, max. rainfall 1600mm) to the northern lowlands (1000m, mean rainfall 300mm). Mpala is situated sufficiently close to the center of this gradient that some of the fauna and flora that are characteristic of either the mesic or xeric end tend to co-occur there. Obvious examples are Grevy's and Plains zebras, and helmeted and vulturine guineafowl (Young *et al*., 1998).

2.2   STUDY SITE

The study was conducted at M.R.C. near the research centers' airstrip, between January and April 2004. The study site was selected as suitable for this investigation because previous studies have shown that the area has a large composition of herbivores, both wild and livestock. The site also has an effective exclusion plot with electric fences that control all large and small herbivores.

The study site comprise one exclusion plot measuring 70m×50m established in 1995 on red soil. At the sites chosen *A. nilotica*, *A. mellifera, A. brevispica* and *A. etbaica* are found. All herbivores have been excluded from this plot by a sixteen-strand

electric fence 2.2 m high. Small herbivores have been excluded using a 45cm-high
wire mesh all around the exclusion (Plate 1). Adjacent to the exclusion are *Acacia*
bushes that are open to herbivore grazing. The study plots comprised the enclosure
and also the adjacent naturally-grazed area at a distance of 100m radially from this
enclosure (Plate 2a and b). Three species of *Acacia* were investigated because they
were the only ones flowering at the time of the investigation. These were *Acacia
brevispica, A. nilotica* and *A. etbaica*. Both livestock and wildlife herbivore
preferences of the *Acacia* species under investigation were considered to be similar.

2.3   GENERAL SAMPLING METHODS

The survey was conducted using three levels of herbivory. These included:

i.   Trees not browsed inside the exclusion plot (Plate 1)

ii.   Trees naturally browsed (Plate 2a and b),

iii.   Trees heavily "browsed" through simulated herbivory outside the plot
(Plate 3). Heavy browsing was simulated by clipping off all leaves from
one branch of the chosen *Acacia* tree using secateurs. Five trees of each
Acacia species were selected randomly. On these five trees, 15 branches,
100cm long from the main stalk, were chosen at random. All the leaves on
each of the branches were individually clipped off between 6-8/1/2004.

Plate 1: Herbivore excluded plot

Plate 2(a) Naturally browsed *Acacia* trees and wild life herbivores

Plate 2(b) Naturally browsed *Acacia* and livestock herbivores

Plate 3: Simulation of herbivory on *Acacia* trees

Trees from within the exclusion plot were treated as not browsed. Samples taken from trees up to a radius of 100m around the exclusion plot were treated as normally browsed by herbivores. Samples taken from the pruned branches within the enclosure were treated as heavily browsed.

Data were collected fortnightly between 19/1/2004 and 23/4/2004. There were 8 sampling sessions each taking 5 continuous days and totaling to 40 sampling days. Samples were taken at fixed time intervals of 1 hour between 08h00 and 12h00, apart from pollinator visitation and pollen release surveys (which both required a whole day of sampling). Samples of flowers for determining changes in inflorescence diameter were always taken at 08h00 and measurement done at 09h00 to avoid variable errors in reading due to loss of water as the tissues dried out.

2.4   DATA COLLECTION

2.4.1   FLOWER ABUNDANCE AND MORPHOMETRY

To determine the number of flowers, florets and anthers produced by *Acacia* trees, branches measuring 50 cm in length of each of the 45 trees (5 trees of each of the 3 *Acacia* spp in each of the 3 treatments) were randomly selected. The number of flowers in each of these branches was counted. A random sample of 400 fresh flowers (100 flowers per sampling session) was taken from each tree under investigation at 08h00. The diameters and weights of these flowers were determined using Cam Lab Vanier calipers and Mettler Toledo AB54 Max 50g Fine Electronic Balance. Of these

same flowers, the number of florets in each inflorescence and the number of anthers in each floret were counted under a Leica M275 Dissecting microscope at ×10 magnification.

2.4.2 POLLEN RELEASE

To quantify pollen release (dehiscence) in each species of *Acacia*, relative abundance method [protocol described by Stone *et al*. (1996)] was used. The pollen present on the surface of inflorescences was quantified at 1-hour intervals throughout the day from 06h00-18h00. Three inflorescences were taken at random from each of the five trees of the three species of *Acacia* in the three (unbrowsed, naturally browsed and heavily browsed) levels of herbivory. Pollen slides were made for each of these inflorescences by rolling it gently across the adhesive side of a piece of clear adhesive tape and placing the tape over a microscope slide. These pollen slides were examined under a Nikon Eclipse E400 compound microscope at ×100 magnification. Observations were made in five randomly chosen microscope fields for each pollen slide. In each field, the number of polyads (compound pollen grains) and anther heads collected on the tape was counted and the means for all the five fields for each slide averaged.

2.4.3 NECTAR

To quantify nectar production in *A. brevispica* known to secrete nectar, a total of 30 florets were randomly taken in each sampling session and nectar presence or absence determined with a 1µl micropipette (Camlab, U.K.). One side of the micropipette was slowly probed into the floral calyx between the anthers. Where possible, nectar volume was determined from the length of the nectar column in the micropipette. Nectar concentration was measured using a hand held sugar refractometer modified

for very low volumes (Bellingham and Stanley, U.K.- Stone *et al.,* 1996). However, attempts to extract nectar from *A. brevispica* were entirely negative and did not yield any substantial volumes; thus no comparisons could be made to establish any effect of herbivory on its production.

2.4.4 POLLINATOR ABUNDANCE

Pollinator visitation to *Acacia* flowers was quantified by watching randomly selected groups of inflorescences (10 inflorescences on one branch per tree) continuously for 30 minutes in each hour of the day (08h00-18h00). The number and type of flower visitors that touched either the anthers or stigma were recorded (McCall and Primack, 1992; Stone *et al.,* 1996). Specimens of flower visitors were captured using sweep nets. The visitors (bees, wasps, flies, butterflies, beetles and other insects) trapped were identified at Mpala Research Centre using a reference collection.

2.4.5 DIVERSITY OF OTHER NECTAR AND POLLEN SOURCES

The wild flower plant species diversity was determined in the study sites on 5 by 5 metre plots (15 plots inside and 15 plots outside the exclusion plot), because their diversity would attract different pollinators, which would in turn visit *Acacia* flowers. Species identity and abundance of all plants that were present in each plot was recorded.

2.5   DATA ANALYSIS

All data are shown as means $\pm$ Standard Error (SE). MINITAB Statistical Program (Release 13 for windows) was used to analyze the data. Normal distribution of the datasets was determined using the normality test before statistical analysis was done.

Analysis of Variance (ANOVA; Townsend, 2002) was used to analyze variation in different flower attributes between the three levels of browsing. Where statistically significant difference were detected ($p<0.05$), maximally non-significant subsets were derived by the Student-Newmann-Keul (SNK) post-hoc test procedure (Townsend, 2002). Pearson Correlation was used to test for association between floral weight and diameter. Chi-Square was used to test the goodness of fit of pollinator abundance inside and outside the enclosure (Townsend, 2002). Pollinator species richness and diversity were determined using the indices of biological diversity using the Shannon–Weiner (H') indices, Berger Parker dominance (d) and species Evenness (J') on Estimates Biodiversity Program version 6.0.

The Kolmogorov Smirnov (KS) test was used to test for temporal shifts, both in visitation peaks between treatments, and in the peaks of pollen release for each species under different treatments.

CHAPTER 3

RESULTS

3.1 FLOWER ABUNDANCE ON DIFFERENT *ACACIA* TREES

The mean number of flowers produced by different *Acacia* trees under different browsing levels, averaged across sampling times are presented in Table 1. Unbrowsed trees of *A. nilotica* and *A. brevispica* trees produced significantly ($P<0.05$) more flowers than naturally browsed and heavily browsed trees (Table 1). On the other hand, heavily browsed trees of *A. etbaica,* produced a similar ($P>0.05$) number of flowers per branch as unbrowsed and naturally browsed trees although unbrowsed trees produced significantly ($P<0.05$) more flowers than naturally browsed trees (Table 1).

Among the three species of *Acacia*, unbrowsed and naturally browsed trees of *A. brevispica* produced significantly ($P<0.05$) more flowers than *A. etbaica* and *A. nilotica*. However, heavily browsed *A. etbaica* produced significantly ($P<0.05$) more flowers per tree than heavily browed *A. brevispica* and *A. nilotica* (Table 1).

Table 1: Mean number of flowers produced per branch of *Acacia* spp. under different browsing levels.

Level of browsing	Number of Flowers on *Acacia* trees (Mean ± SE)		
	A. nilotica	*A. brevispica*	*A. etbaica*
Unbrowsed	4.30 ± 0.15 Ac (n=200)	12.14 ± 0.61 Aa (n=200)	5.43 ± 0.71 Ab (n=150)
Browsed	4.05 ± 0.17 Bb (n=190)	5.27 ± 0.22 Ba (n=200)	3.80± 0.57 Bc (n=150)
Heavily browsed	1.64 ± 0.12 Cb (n=50)	1.82 ± 0.15 Cb (n=70)	4.72 ± 1.12 ABa (n=70)

Means ± SE in the same column followed by the same upper case alphabetical letter(s) are not significantly different (P=0.05) by SNK.

Means ± SE in the same row followed by the same lower case alphabetical letter(s) are not significantly different (P=0.05) by SNK.

3.2 FLOWER DIAMETER

Variations in inflorescence diameter under the three levels of browsing indicate that unbrowsed trees of *A. nilotica* produced significantly (P<0.05) larger diameters than naturally browsed and heavily browsed trees (Table 2).

Unbrowsed *A. brevispica* trees also produced significantly (P<0.05) larger flowers than naturally browsed and heavily browsed trees, whose floral diameters were not different (P>0.05 – Table 2). On the other hand, heavily browsed *A. etbaica* trees produced significantly (P<0.05) larger floral diameters than unbrowsed trees. Naturally browsed tree of this species produced flowers with diameters similar to both the heavily browsed and unbrowsed trees (P>0.05 - Table 2).

Comparing floral diameters in the three *Acacia* species, assuming that they are similar phenotypically, unbrowsed *A. nilotica* produced flowers with significantly (P<0.05) smaller diameters than unbrowsed *A. brevispica* and *A. etbaica,* which both produced flowers whose diameters were not different (P>0.05). On the other hand, naturally and heavily browsed trees of *A. etbaica* produced significantly (P<0.05) larger floral diameters than naturally and heavily browsed trees of *A. nilotica* and *A. brevispica* (Table 2).

Table 2: Mean flower diameter of *Acacia* spp. under different browsing levels

	Floral diameters of *Acacia* species (Mean ± SE)		
Level of browsing	*A. nilotica*	*A. brevispica*	*A. etbaica*
Unbrowsed	1.22cm ± 0.01 Ab (n=400)	1.34cm ± 0.01 Aa (n=350)	1.32cm ± 0.01 Ba (n=400)
Browsed	1.05cm ± 0.02 Bc (n=400)	1.14cm ± 0.02 Bb (n=350)	1.37cm ± 0.02 ABa (n=400)
Heavily browsed	0.84cm ± 0.02 Cc (n=56)	1.12cm ± 0.01 Bb (n=75)	1.38cm ± 0.01 Aa (n=400)

Means ± SE in the same column followed by the same upper case alphabetical letter(s) are not significantly different (P=0.05) by SNK.

Means ± SE in the same row followed by the same lower case alphabetical letter(s) are not significantly different (P=0.05) by SNK.

3.3   RELATIONSHIP BETWEEN FLOWER DIAMETER AND WEIGHT.

a) *Acacia nilotica.*

Unbrowsed trees had a highly significant positive correlation between their floral diameters and corresponding weights correlation (r_{398}=0.39, P<0.01-Fig. 2). Similarly, a significant positive relationship between floral weights and floral

diameters was recorded for both naturally browsed (r_{398}=0.59, P<0.01) and heavily

browsed trees (r_{398}=0.78, P<0.01).

b) *Acacia brevispica*.

A significant positive correlation (r_{349}=0.72, P<0.01, =0.90, P<0.01, and r_{73}=0.46,

P<0.01-Fig.2) between floral weight and diameter was recorded for *A. brevispica*

trees in the three (unbrowsed, naturally browsed and heavily browsed respectively)

levels of browsing.

c) *Acacia etbaica.*

A. etbaica trees in all the three levels of browsing also showed a positive linear

correlation between inflorescence diameter and weights. Unbrowsed trees had a very

strong positive association (r_{398}=0.67, P<0.01), followed by naturally browsed trees

(r_{398}=0.28, P<0.01) and heavily browsed trees (r_{398}=0.26, P<0.01, Fig.2).

Pearson correlation of flower weights and diameters of *Acacia* trees under different browsing levels
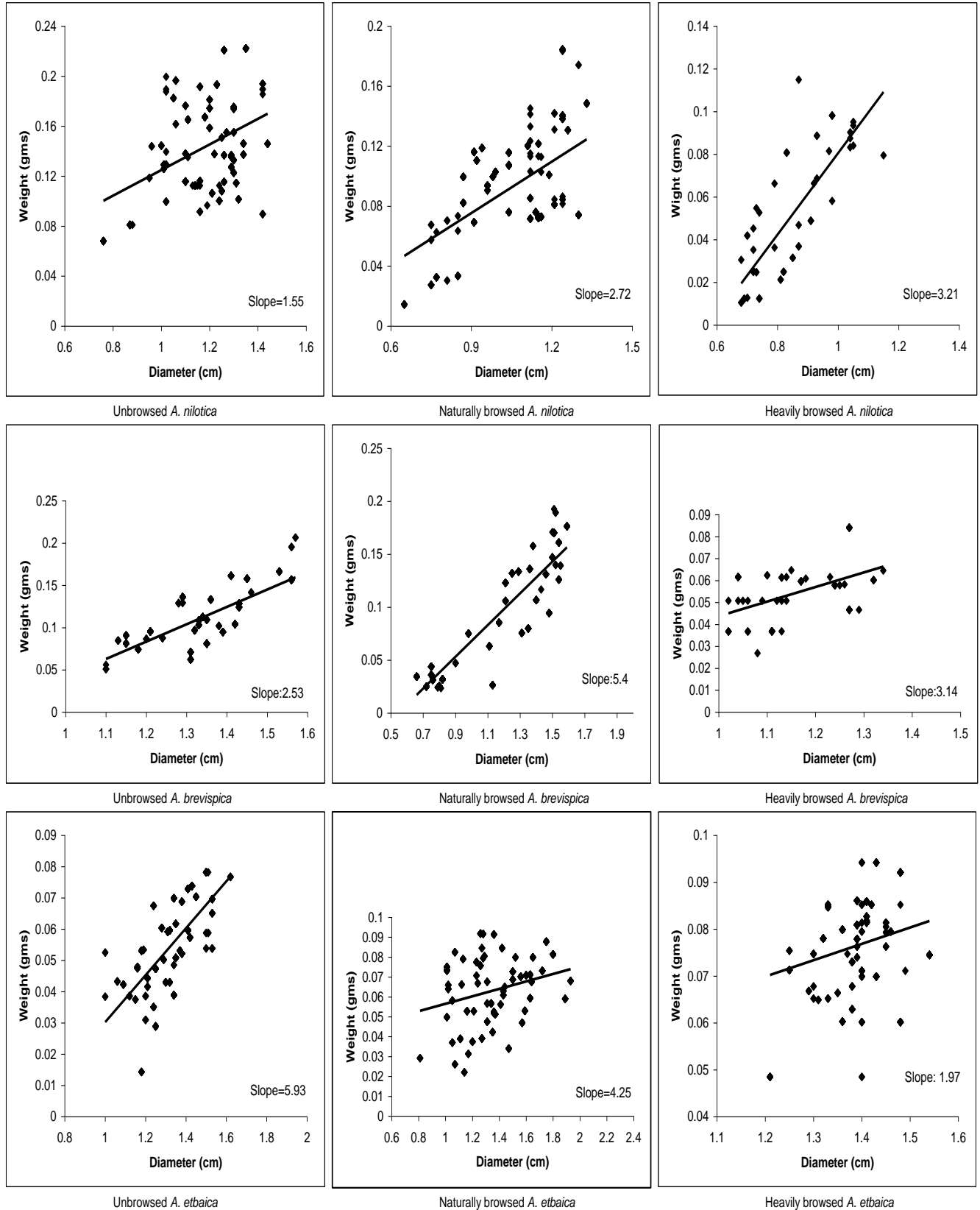
Figure 2: Pearson correlation of flower weights against diameters for different *Acacia* spp. under different browsing levels.

3.4   FLORET NUMBERS

Heavily browsed *A. etbaica* trees produced significantly (P<0.05) more florets in each inflorescence than naturally browsed and unbrowsed trees (Table 3). Heavily browsed *A. brevispica* trees produced significantly (P<0.05) fewer florets in each inflorescence than naturally browsed and unbrowsed trees which both produced the same (P>0.05) number of florets per inflorescence. Unbrowsed trees of *A nilotica* produced significantly (P<0.05) more florets in each inflorescence than naturally browsed and heavily browsed trees which both produced a similar (P>0.05) number of florets.

The number of florets produced by naturally browsed *A. nilotica* was significantly (P<0.05) more than both naturally browsed *A. brevispica* and *A. etbaica*, which produced the same (P>0.05) number of florets per inflorescence. On the other hand, unbrowsed and heavily browsed *A. nilotica* trees produced significantly (P<0.05) more florets per inflorescence than *A. brevispica* and *A. etbaica* (Table 3).

Table 3: Mean number of florets per inflorescence of different *Acacia* spp. under different browsing levels.

Level of browsing	Floret numbers per inflorescence of *Acacia* species (Mean ± SE)		
	A. nilotica	*A. brevispica*	*A. etbaica*
Unbrowsed	114±0.81 Aa (n=400)	30.6±0.30 Ab (n=350)	28.8±0.30 Cc (n=400)
Browsed	75.2±1.24 Ba (n=400)	30.3±0.25 Ab (n=350)	30.1±0.27 Bb (n=400)
Heavily browsed	77.2±0.60 Ba (n=56)	18.6±0.46 Bc (n=75)	32.6±0.20Ab (n=400)

Means ± SE in the same column followed by the same upper case alphabetical letter(s) are not significantly different (P=0.05) by SNK.

Means ± SE in the same row followed by the same lower case alphabetical letter(s) are not significantly different (P=0.05) by SNK.

3.5 VARIATION IN ANTHER PRODUCTION

A summary of the number of anthers produced per floret of Acacias that were studied is presented in Table 4. Naturally browsed trees of *A. nilotica* produced significantly (P<0.05) less anthers in each floret than unbrowsed and heavily browsed trees, which produced a similar (P>0.05) number of anthers in their florets (Table 4). On the other hand, naturally browsed *A. brevispica* produced significantly (P<0.05) more anthers than unbrowsed and heavily browsed trees while heavily browsed *A. etbaica* trees produced significantly (P<0.05) more anthers than both naturally and heavily browsed trees.

Acacia brevispica trees produced significantly (P<0.05) more anthers per floret than *A. nilotica* and *A. etbaica*, which also significantly differed (P<0.05) between themselves in the three levels of herbivory (Table 4).

Table 4: Mean number of anthers per floret of different *Acacia* spp. under different browsing levels.

Level of browsing	Number of anthers per floret of *Acacia* species (Mean ± SE)		
	A. nilotica	*A. brevispica*	*A. etbaica*
Unbrowsed	56.5±0.41 Ab (n=400)	61.4±0.54 Ba (n=400)	39.1±0.44 Cc (n=400)
Browsed	54.4±0.56 Bb (n=400)	62.9±0.33 Aa (n=400)	42.4±0.62 Bc (n=400)
Heavily browsed	56.8±0.41 Ab (n=400)	59.3±0.34 Ca (n=400)	50.9±0.29 Ac (n=400)

Means ± SE in the same column followed by the same upper case alphabetical letter(s) are not significantly different (P=0.05) by SNK.

Means ± SE in the same row followed by the same lower case alphabetical letter(s) are not significantly different (P=0.05) by SNK.

3.6   FLOWER VISITATION AND POLLINATOR DIVERSITY

4.5.1   FLOWER VISITATION

a) *Acacia nilotica.*

Pollinator activity was recorded across the day (12 hours) on both unbrowsed and naturally browsed *A. nilotica* trees (Figure 3a). Pollinator visitation to unbrowsed *A. nilotica* started at lower frequencies early in the morning and had a steady increase until it peaked (41 visits) between 10h00-11h00. It then started to decline steadily until it was 0 between 17h00-18h00 when the flowers had begun to wither and change colour from bright to pale yellow.

Naturally browsed trees followed a different trend. Far lower visitation frequencies were recorded for these trees, with peak pollinator activity occurring later in the day between 12h00-13h00 (Fig. 3a). The peak pollinator activity on unbrowsed trees occurred significantly (KS =2.89, p<0.01) earlier (between 10h00 and 11h00) than on naturally browsed trees (12h00-13h00) of *A. nilotica* (Fig. 3a).

Bees had the highest frequency of visitation among all the pollinators recorded for unbrowsed *A. nilotica* trees (Fig 3b), constituting 73.3% (Appendix 1), of the total visits across the day. Flies followed bee activity as the second most important visitor constituting 11.2% of the total visits. Beetles constituted 4.4%, wasp 5.9% and other pollinators 5.2 % (Appendix 1) of the total visits to the unbrowsed trees.

Similar pollinator proportions were recorded for naturally browsed *A. nilotica* trees (Fig 3c), with bees constituting the largest proportion of total visits (62%) followed by beetles (19.9%) and flies (11%) (Appendix 1). Other pollinators constituted 7.1% of

the total visits to these trees. Bee and beetle activities both peaked between 12h00-

13h00 (Figure 3c), and were clearly responsible for the overall shifts in visitor

frequency seen between unbrowsed and browsed trees. Heavily browsed trees

produced very few flowers that were open and receptive at the time of pollinator

activity surveys, hence no pollinators were recorded for these trees.
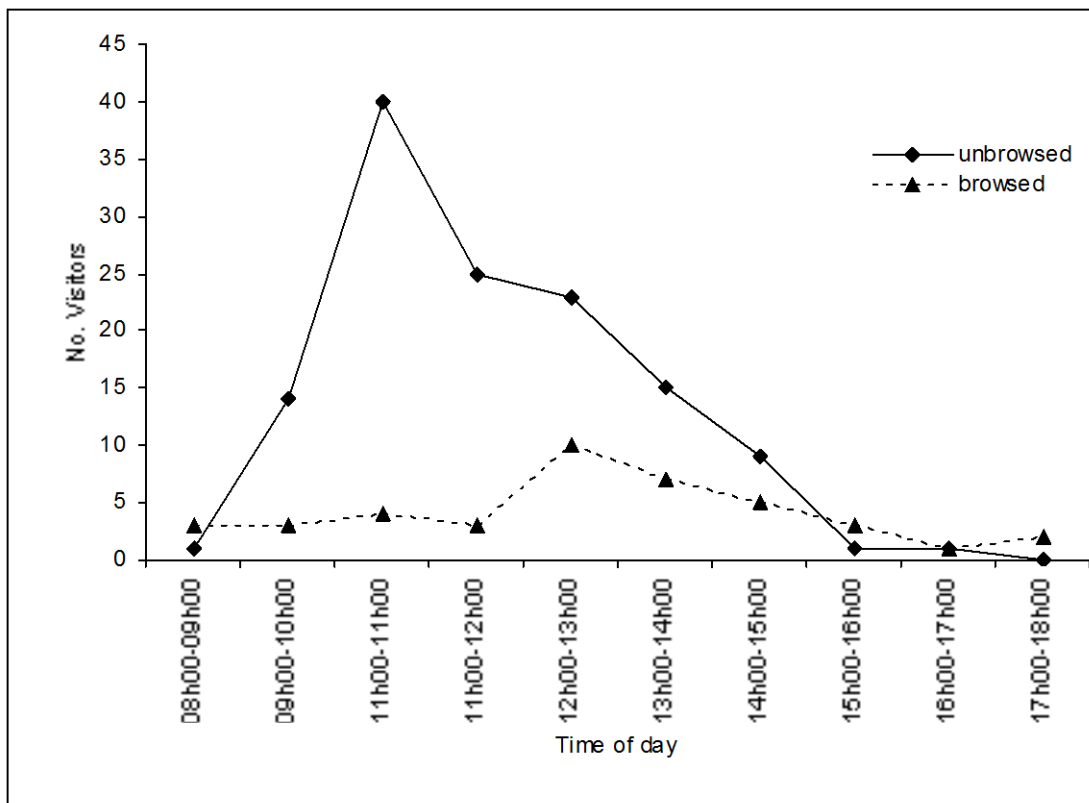
Figure 3(a): Pollinator activity on unbrowsed and naturally browsed *A. nilotica* trees per hour across the day.
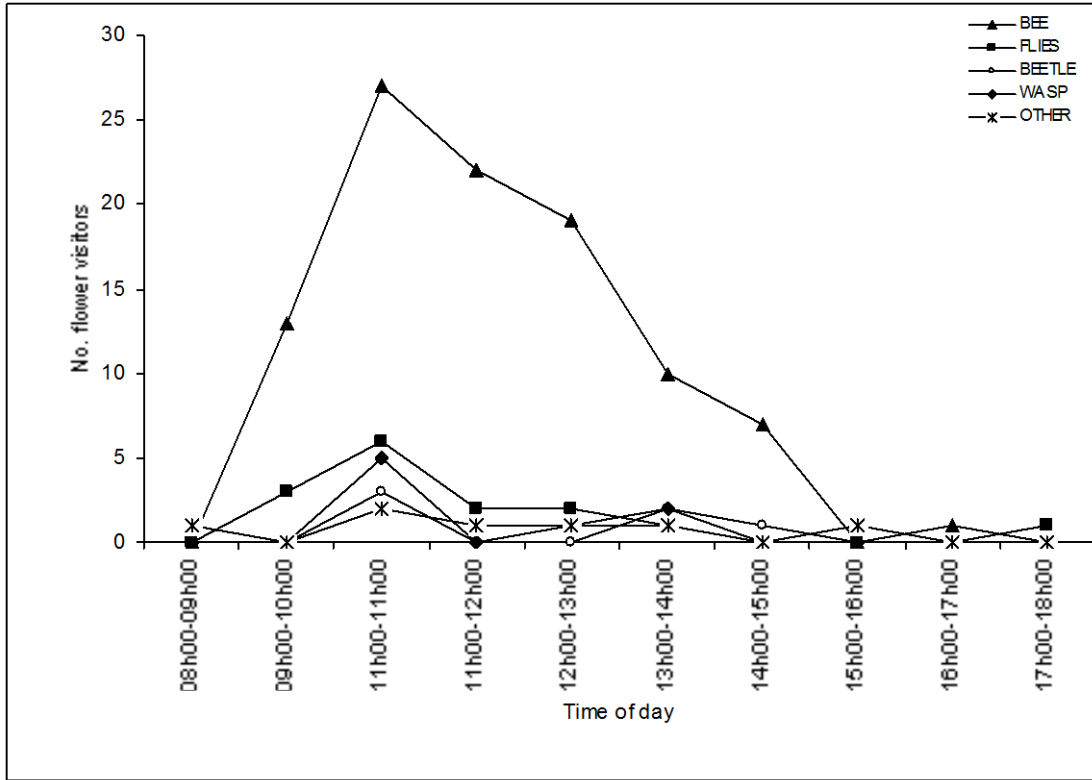
Figure 3(b): Patterns of pollinator activity by insect guild to unbrowsed *A. nilotica* trees.
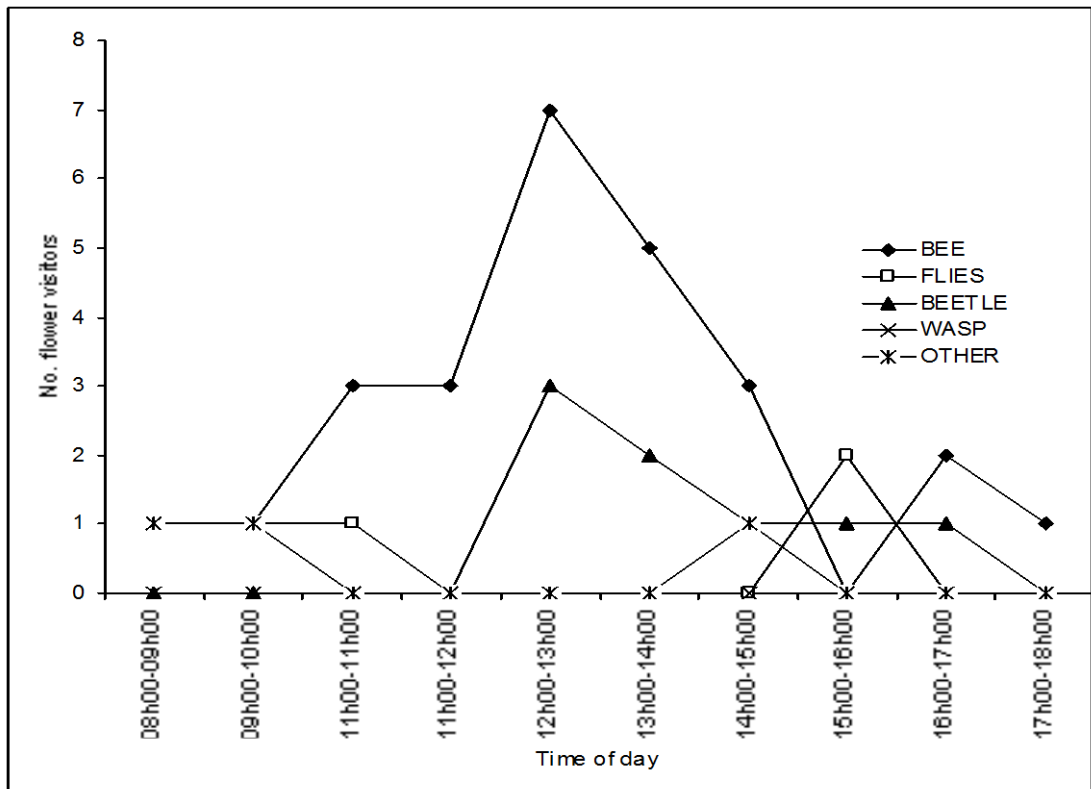
Figure 3 (c): Patterns of pollinator activity by insect guild to naturally browsed *A. nilotica* trees.

b) *Acacia brevispica.*

Pollinator activity on unbrowsed and naturally browsed *A. brevispica* trees is

represented in Figure 4(a). Pollinator activity on unbrowsed *A. brevispica* peaked

earlier in the day between 10h00-11h00 then began to decline steadily across the day.

Conversely, activity of pollinators on naturally browsed trees remained at low

frequencies with a slight peak between 16h00-17h00. Very low pollinator visitation

rate was recorded between 13h00-14h00 for both unbrowsed and naturally browsed

trees, increasing slightly again after 14h00pm.
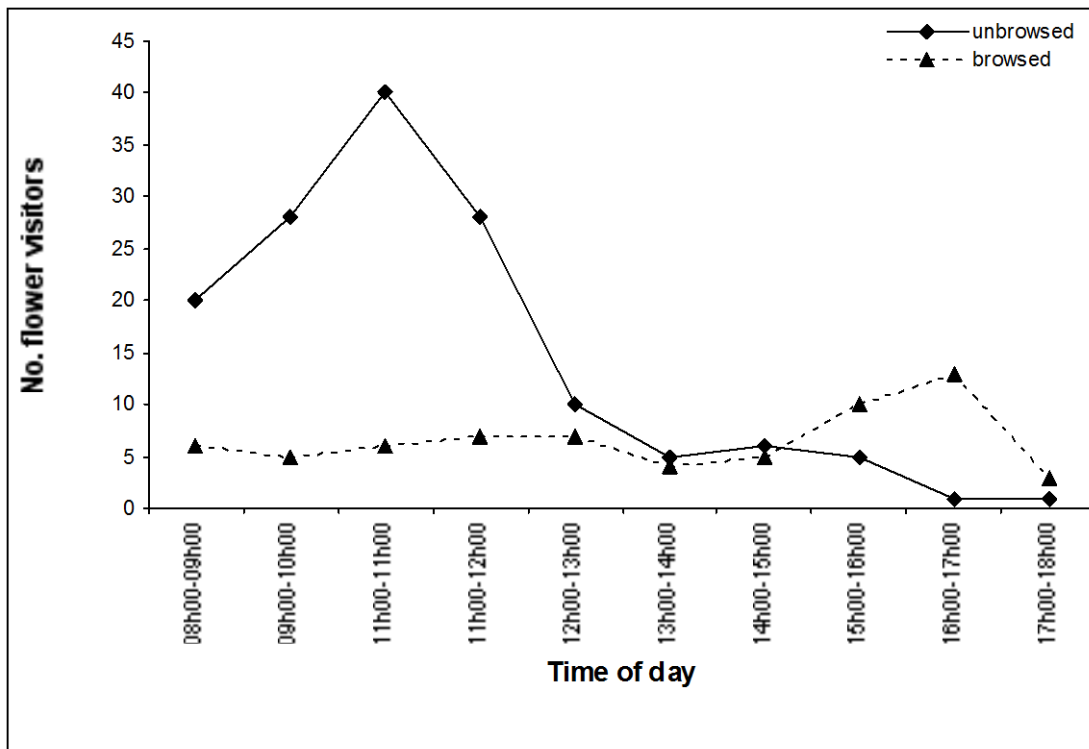
Figure 4(a): Pollinator activity on unbrowsed and naturally browsed *A. brevispica* trees across the day.

The most frequent and abundant pollinator guild to unbrowsed trees was the bee,

constituting 49.3% of the total visits (Appendix 1). Bee activity peaked between

10h00-11h00 (Fig. 4b) before beginning a steady decline as the day progressed while

flies formed 40.2%, beetle 5.6%, wasp 1.4% with other pollinators constituting 3.5% of the total visits to these trees.
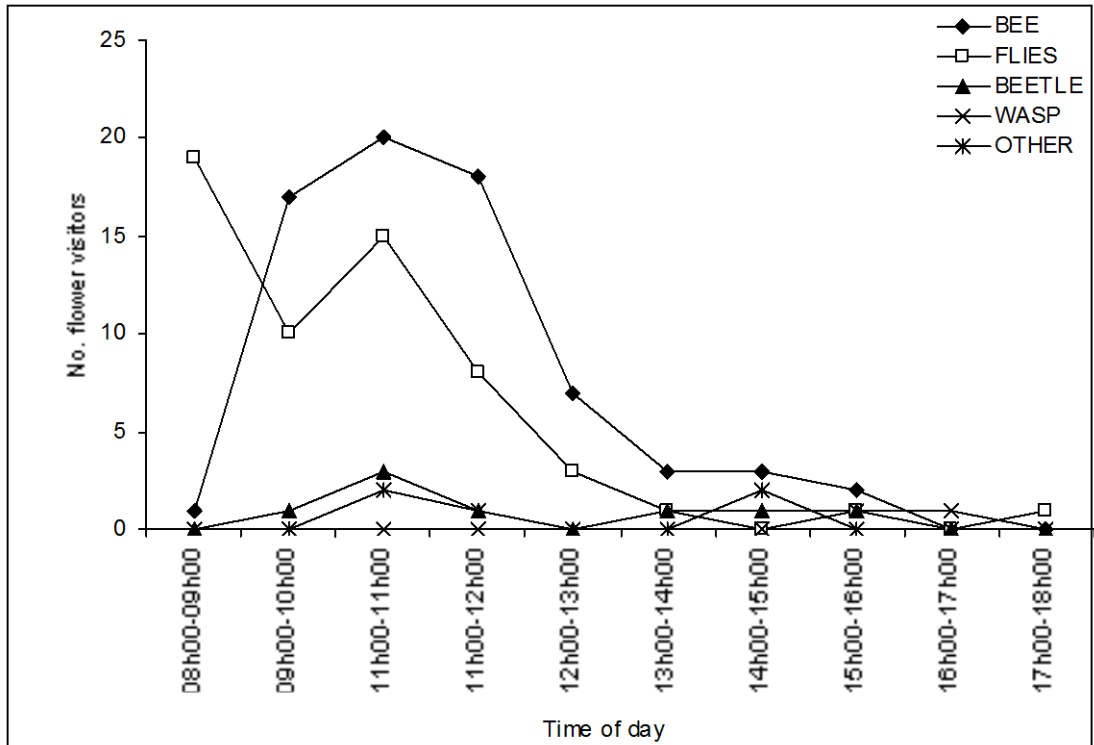
Figure 4(b): Patterns of pollinator activity by insect guild to unbrowsed *A. brevispica* trees.

Patterns of pollinator activity on naturally browsed trees showed that the major constituents were bees and flies. Bees had the highest frequency of visits (50%) and their peak activity was recorded between 16h00-17h00 (Figure 4c). Fly visitation frequency followed bee activity closely (40.9%), beetles (3%) and other pollinators constituted 6.1% of the total visits (Appendix 1).
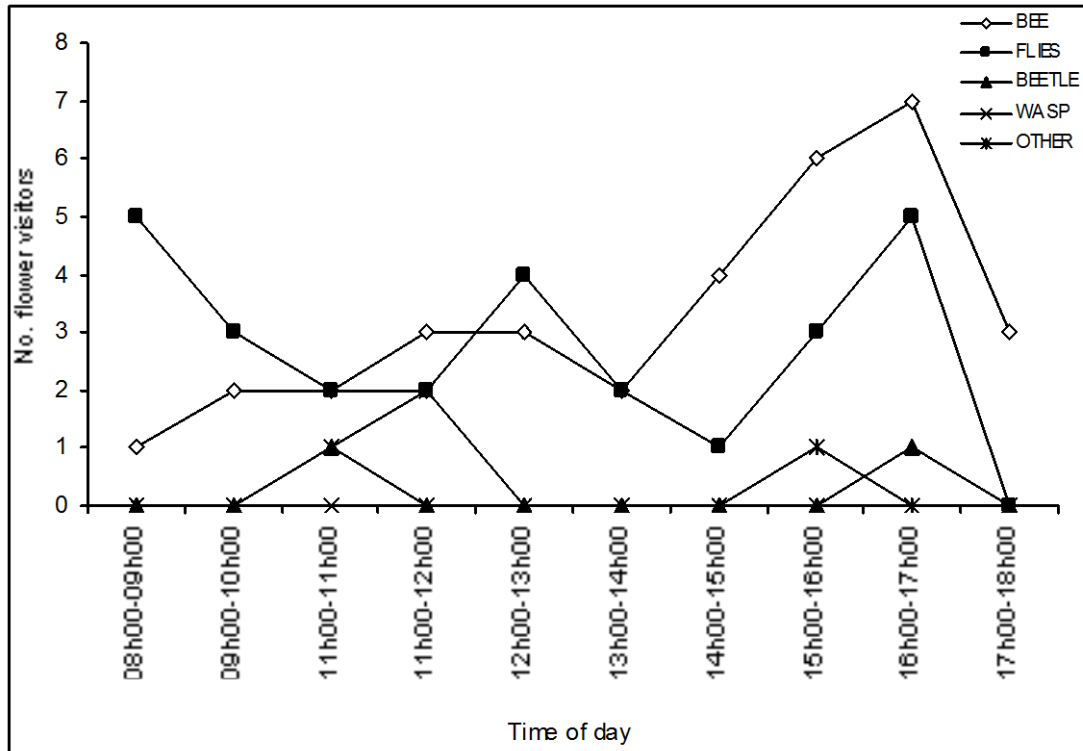
Figure 4(c): Patterns of pollinator activity by different insect guilds to naturally browsed *A. brevispica* trees.

Similar to *A. nilotica,* heavily browsed *A. brevispica* trees produced very few flowers, and even fewer that were open and receptive at the time of pollinator visitation survey, therefore, no pollinator activity was recorded for these trees.

Peak pollinator activity on unbrowsed and naturally browsed trees again differed significantly with time of day (KS = 0.315, P<0.01), generally showing that unbrowsed trees reached an earlier peak of pollinator activity than naturally browsed trees.

c) *Acacia etbaica.*

Figure 5(a) is a summary of total pollinator activity on *A. etbaica* trees under different browsing levels. For this species, total numbers of pollinators visiting unbrowsed,

naturally and heavily browsed *A. etbaica* trees did not differ, although the timing of visits did vary. Unbrowsed trees had two peaks of pollinator activity, one between 10h00-11h00 and the other one between 14h00-15h00. Naturally browsed trees had only one visitation peak between 12h00-13h00, whereas heavily browsed trees had peak pollinator activity between 14h00-15h00.

The patterns of activity by particular groups of pollinators are presented on Fig. 5(b). Bees constituted the highest proportion of pollinators that visited unbrowsed trees (58.3%) while flies constituted 8.3%, beetles 6.3%, wasp 8.3% and other pollinators formed 18.8% of the total visits (Appendix 1).
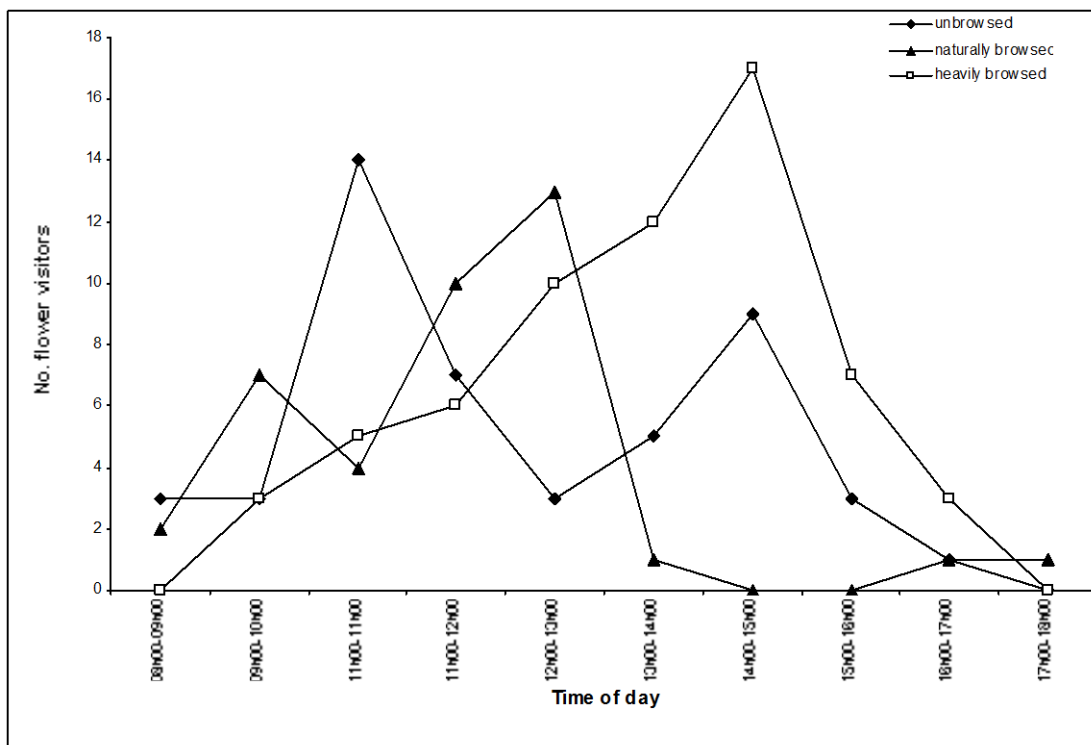
Figure 5(a): Pollinator activity on unbrowsed, naturally browsed and heavily browsed *A. etbaica* trees across the day.
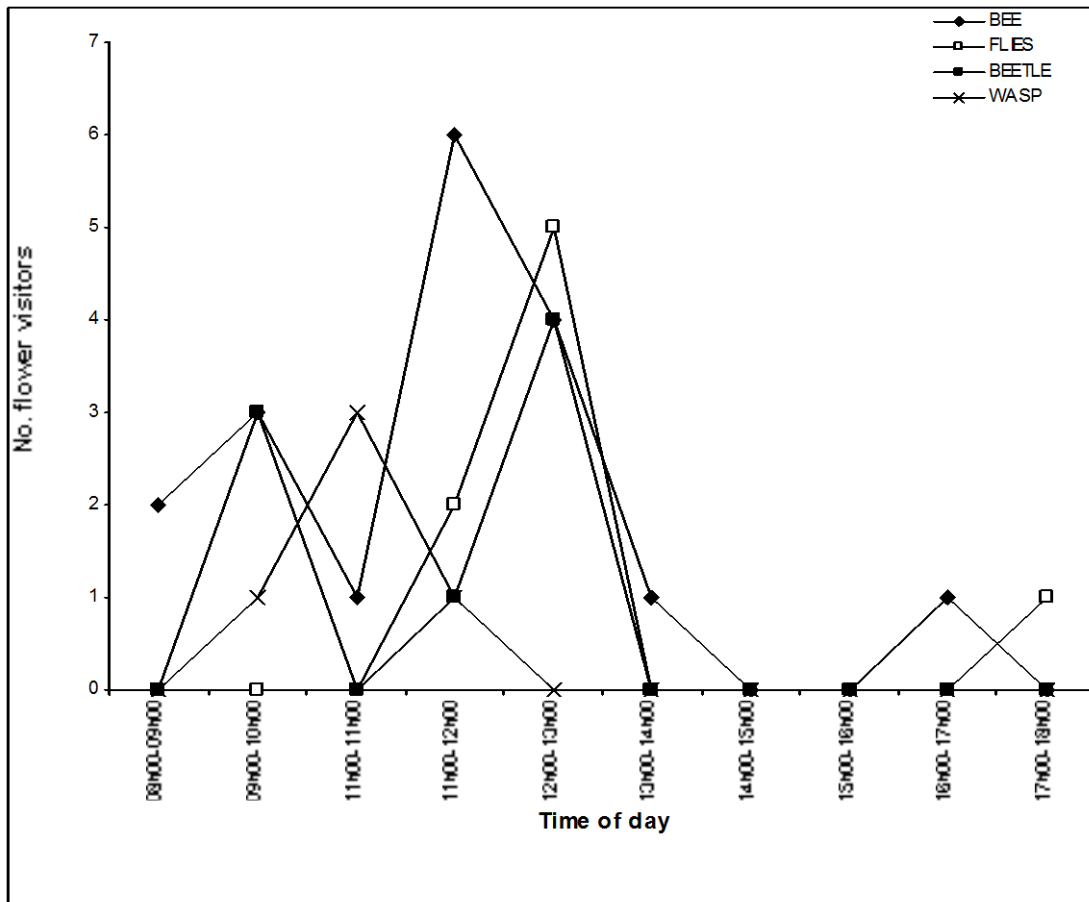
Figure 5(b) Mean daily visitation by different pollinators to unbrowsed *A. etbaica* trees

Summaries of daily visitation by different pollinators to naturally and heavily

browsed *A. etbaica* trees are presented in Fig. 5(c) and 5(d). Major constituents of

pollinators that visited naturally browsed trees were bees, flies and beetles. Bees had

the highest frequency of visits (46.2% - Appendix 1) and their peak activity was

recorded between 11h00-12h00 (Fig. 5c). Flies and beetles formed 20.5% each of the

total visits but flies reached an earlier visitation peak (10h00-11h00 – Fig. 5c) than

beetles, which reached peak activity at the same time as bees (14h00-15h00 – Fig. 5c)

while wasp visitation accounted for 12.8% (Appendix 1) reaching peak activity

between 11h00-12h00 (Fig. 5c).
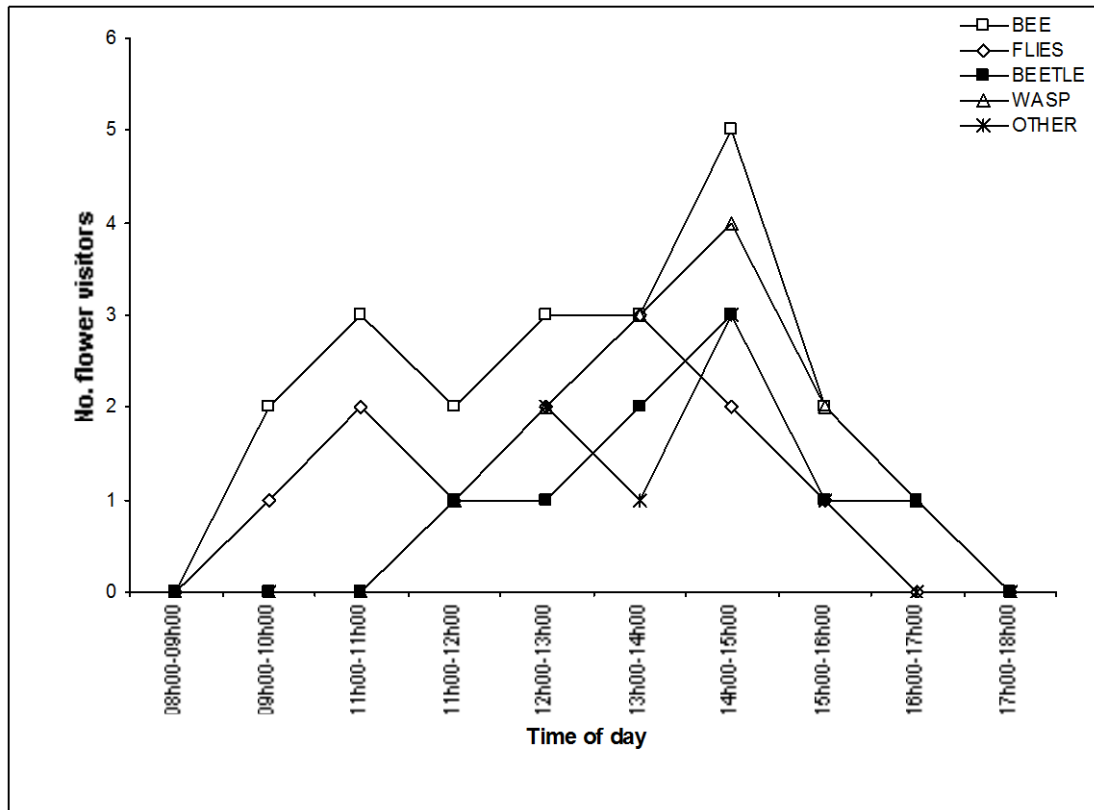
Figure 5(c) Mean daily visitations by different pollinators to naturally browsed *A. etbaica* trees.

Bee visitation to heavily browsed trees accounted for the highest number of visits (33.3% - Appendix 1), followed by wasps (20.6%), flies (19.1%), beetles (14.3%) while other pollinators accounted for 12.7% (Appendix 1). All the pollinators had peak activity between 14h00 and 15h00 (Fig. 5d).
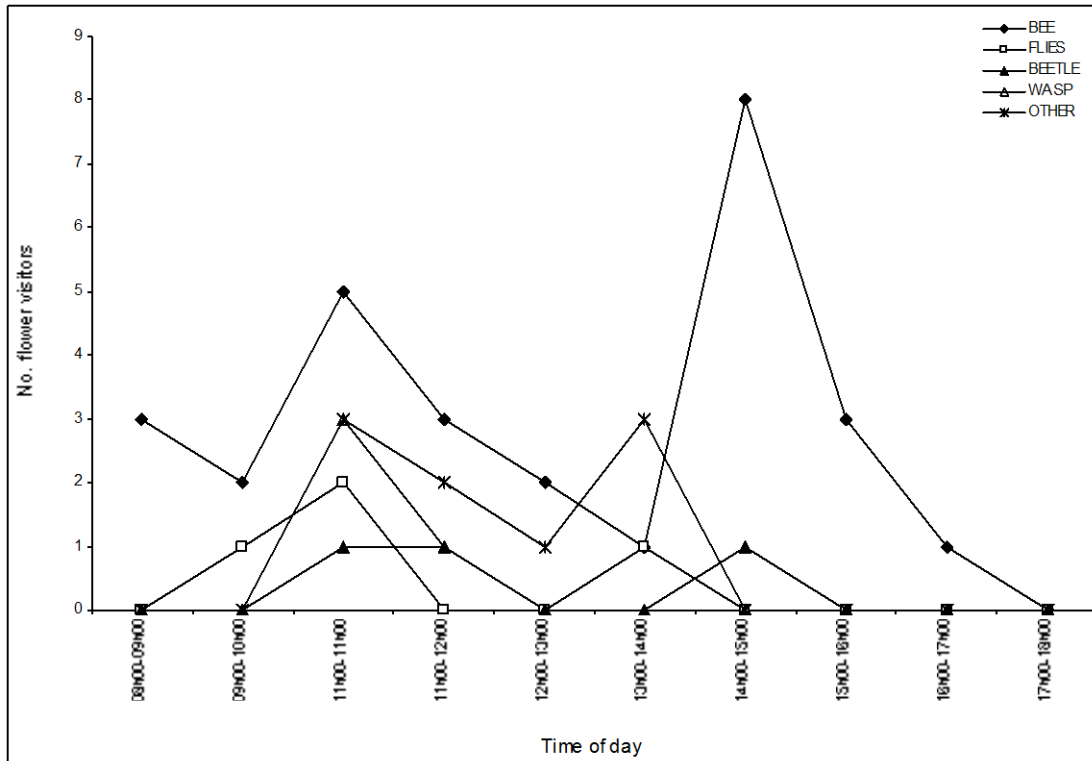
Figure 5(d) Mean daily visitation by different pollinators to heavily browsed *A. etbaica* **trees.**

Pollinator activity on unbrowsed trees occurred significantly earlier than on naturally browsed and heavily browsed trees (KS = 0.22, P<0.01). Most important was the shift in peak between unbrowsed and naturally browsed trees, these peaks occurring at 10h00-11h00 and 12h00-13h00 respectively (Fig. 5a). Thus, for all three *Acacia* species, there were significant differences in pollinator behaviors after trees had been browsed. In each case, peak activity shifted later in the day where a tree had been browsed [compare Figures 3(a), 4(a) and 5(a)], and the effect was mainly due to the shifting activity of bees in each case.

4.5.2 POLLINATOR DIVERSITY

Pollinator diversity was investigated inside and outside the enclosure. Generally, a higher number of pollinators was collected inside the enclosure than outside (Figure 6).
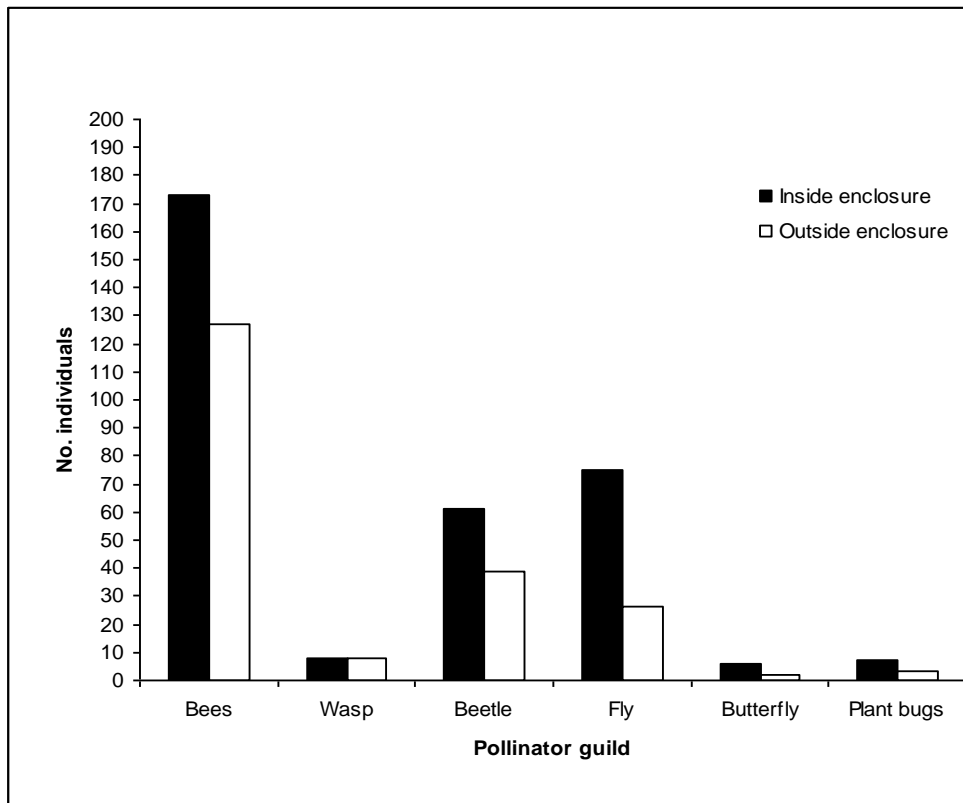
Figure 6: Pollinator diversity by guild inside and outside the enclosure.

The most common pollinators encountered were bees, particularly honeybees. These bees were significantly ($\chi^2 = 7.9$, P<0.01, df=1) more inside the enclosure than outside. Similarly, significantly ($\chi^2 = 19.96$, P<0.01, df=1) more flies were recorded inside the enclosure than outside. Wasps, butterflies and bugs were extremely rare. The abundance of wasps inside the enclosure was similar ($\chi^2 = 0.07$, P>0.05, df=1) to that outside the enclosure represented mainly by the family Eumenidae (potter wasps). Butterflies, mainly consisting of nymphalids and lycaenids, and Plant bugs, mainly

consisting of Pyrrhochorids, also had a similar (χ^2= 2.28, P>0.05, df=1; χ^2=1.46, P>0.05, df=1, respectively) abundance inside and outside the enclosure (Appendix 2).

A total of 535 insect pollinators representing 24 families were recorded both inside and outside the enclosure with more insects inside than outside as shown in (Appendix 2). Apidae was the most abundant insect family inside and outside the enclosure. Parasitoid wasps (braconid and ichnenumonid groups) were only recorded outside the enclosure.

Apis mellifera (Apidae) was the most abundant bee species both inside and outside the enclosure (Appendix 3). Strikingly, halictid bees were mainly collected inside the enclosure, and consisted mostly of *Lipotriches* sp than outside. Megachilid bees were neither abundant inside the enclosure nor outside (Appendix 3).

Based on the Shannon-Wiener diversity index (H^1), the two sites (inside and outside enclosure) were very similar in diversity of pollinator species (Table 5), although slightly more diversity was recorded inside the enclosure than outside.

Table 5: Pollinator species diversity indices inside and outside herbivore-excluded plot

Species diversity index	Inside enclosure	Outside enclosure
Shannon Wiener (H)	0.94	0.82
Eveness (J)	1.3	1.13
Berger-Parker Dominance (d)	0.47	0.58

However, more heterogeneity and diversity was recorded within the enclosure than outside (Table 5). Species were more even inside the enclosure in terms of species distribution than outside (Table 5).

3.7 PATTERNS OF POLLEN RELEASE AND TIMING

a) *Acacia nilotica.*

Dehiscence in unbrowsed *A. nilotica* inflorescences was already occurring when sampling began at 08h00 (Figure 7), and pollen availability continued to be steady until about 10h00-11h00, and started reducing thereafter as pollinators removed the polyads, with pollinator activity stopping completely at 16h00. In contrast, naturally browsed trees had very little dehiscence at 08h00, and reached a peak of dehiscence around 09h00-10h00.
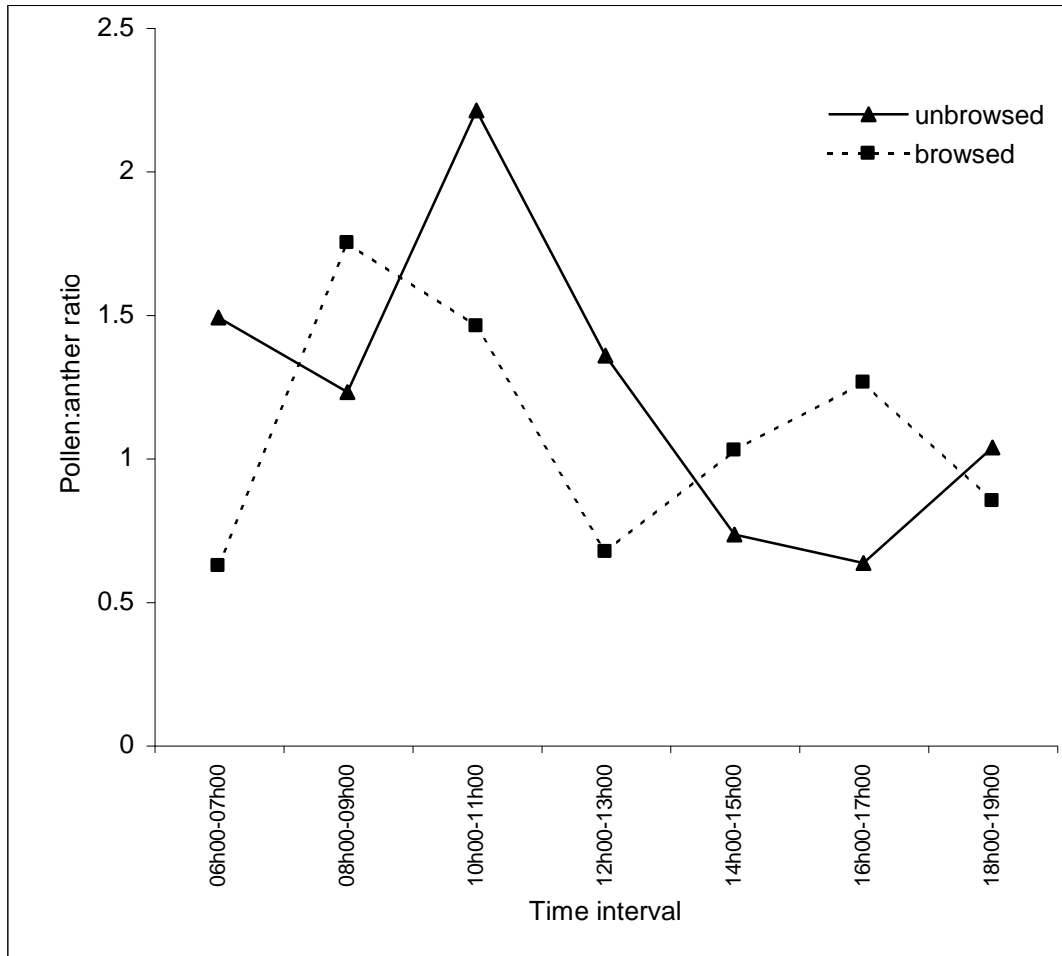
Figure 7: patterns of pollen release on unbrowsed and browsed *A. nilotica* trees

A significant shift in inflorescence dehiscence time was recorded between unbrowsed and browsed trees across the day (KS = 0.34, P<0.01), which means that peak floral dehiscence of naturally browsed trees occurred significantly earlier than on unbrowsed trees.

b) *Acacia brevispica*.

As with *A. nilotica* trees, pollen presentation in unbrowsed *A. brevispica* had a peak dehiscence somewhat earlier than for browsed trees (Figure 8). For unbrowsed trees, the peak was between 12h00 and 13h00, whilst naturally browsed trees had a

dehiscence peak between 14h00-15h00 before declining sharply as pollinators

harvested pollen until 16h00.
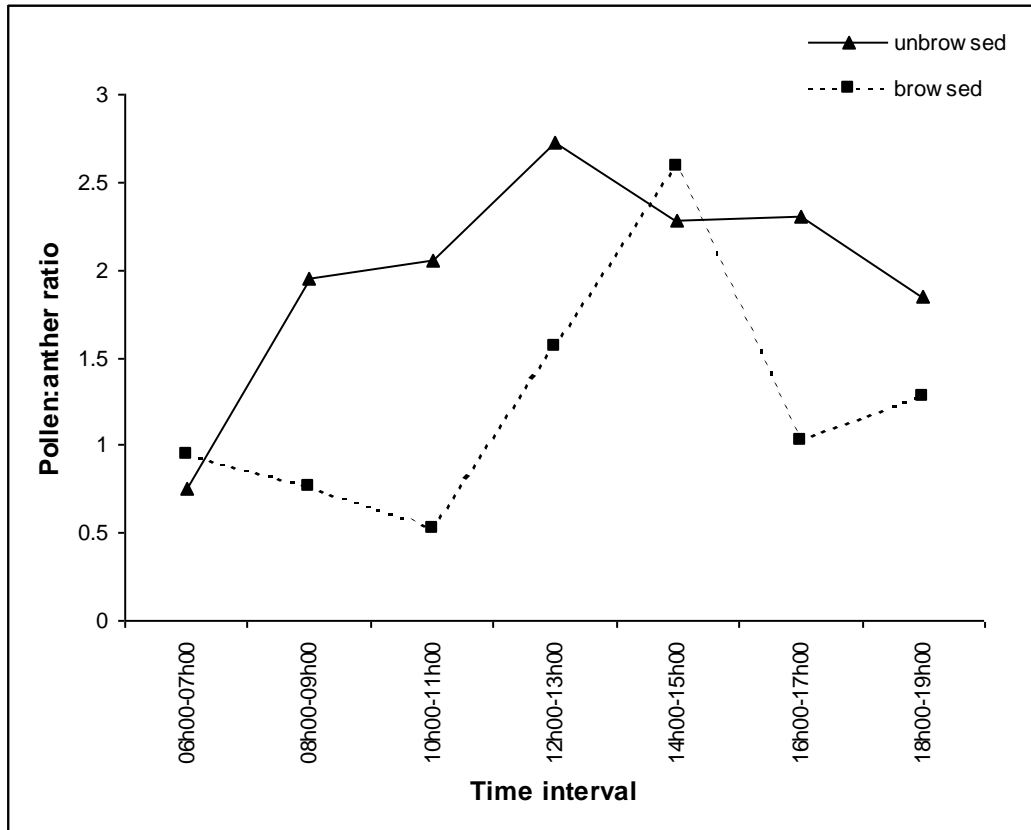
Figure 8: Patterns of pollen release in unbrowsed and naturally browsed *A. brevispica* **trees.**

Again, a highly significant shift of inflorescence dehiscence time was found between

unbrowsed and naturally browsed trees (KS = 0.33, P<0.01), which means that peak

floral dehiscence of unbrowsed trees occurred significantly earlier than on naturally

browsed trees.

 c) *Acacia etbaica***.**

Patterns of pollen release in *A. etbaica* across the day under different browsing levels

are presented in Figure 9. Similar to *A. brevispica*, unbrowsed trees of *A. etbaica*

reached a peak dehiscence at midday; this was a very sharp peak, with pollen:anther ratios nearing the maximum value of 8 (the number of polyads per anther head for this species). However there was no clear peak for the browsed trees, though they reached a dehiscence maximum at 14h00.
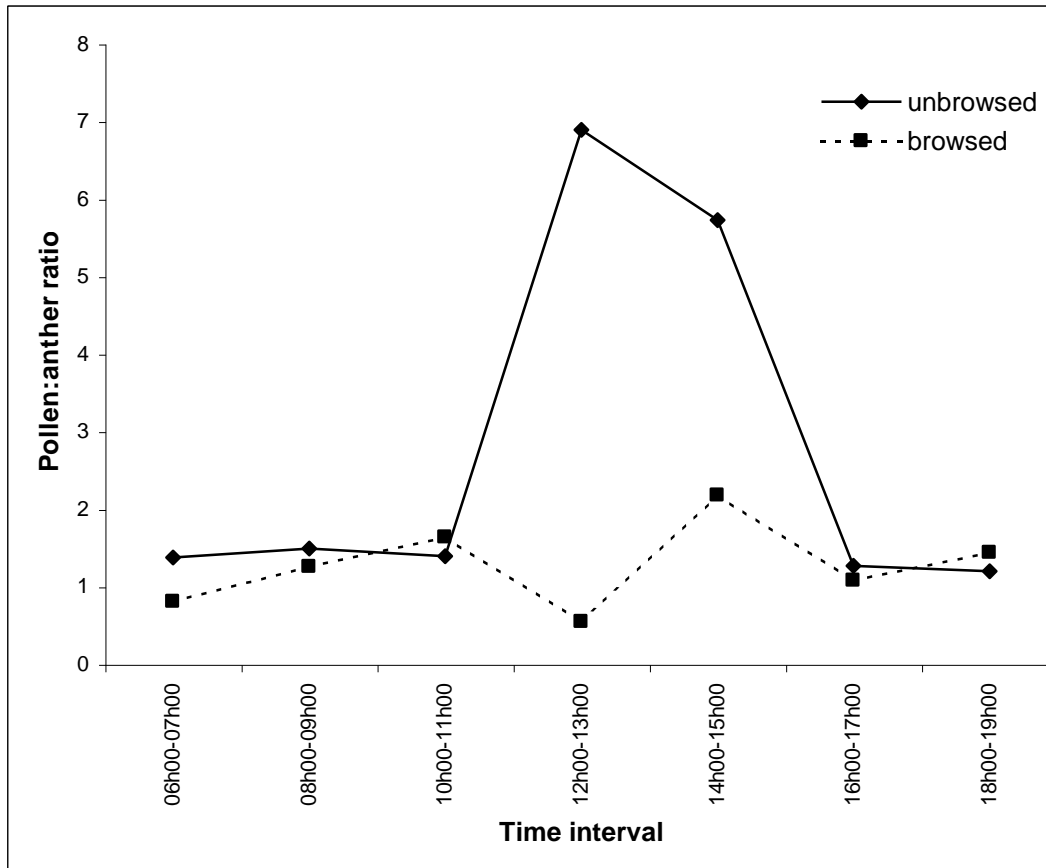
Figure 9: Patterns of pollen release on unbrowsed and naturally browsed *A. etbaica* trees.

A significant shift in inflorescence dehiscence time was recorded between unbrowsed and naturally browsed trees and browsed trees across the day (KS = 0.36, P<0.01), which means that peak floral dehiscence of naturally browsed trees occurred significantly earlier than on unbrowsed trees.

3.8   WILD PLANT SPECIES DIVERSITY

Generally, more species of wild plants were recorded outside the enclosure (S=25) than inside enclosure (S=20). Similarly, greater species diversity was recorded outside than inside the enclosure (Table 6). Species were also more evenly distributed outside than inside the enclosure (Appendix 4). The most dominant plant species outside the enclosure was *Hypoestes* sp. while inside was *Kalanchoe schweinfurthii* (Appendix 4). The latter species was largely responsible for the greater total number of plants recorded inside the enclosure (Appendix 4); which appeared to grow particularly well when released from grazing pressure.

Table 6: Wild plant species diversity indices inside and outside the enclosure.

Species diversity index	Inside enclosure	Outside enclosure
Shannon Wiener (H)	0.62	1
Eveness (J)	0.81	1.4
Berger-Parker Dominance (d)	0.8	0.17

CHAPTER 4

DISCUSSION

4.1 FLOWER ABUNDANC AND DIAMETER

Acacia brevispica trees seem to increase in flower production following herbivore exclusion. Since the leaves are not nibbled by herbivores, more photosynthetic material is available, increasing the rate of primary production. The plants therefore, have more energy to increase their reproductive capacity by investing in production of more flowers to increase reproductive success. Plants with more and conspicuous flowers would recruit more pollinators, thereby increasing their chances of reproduction (Willmer and Stone, 1997).

In contrast, *A. nilotica* and *A. etbaica* did not seem to respond to exclusion of herbivores by increasing floral production substantially (although note that when artificially heavily browsed, *A. nilotica* did show reduced flower number). Instead, *A. nilotica* responded to normal and severe herbivory by reducing the diameter of flower heads. It is possible that when a plant's photosynthetic surfaces are removed, the net energy harnessed is lower and therefore, the resulting growth of parts synchronously become smaller, flower diameter included (Howe and Westley, 1988; Rosenthal and Berenbaum, 1992; Marquis and Whelan, 1994). This reponse of *A. nilotica* may therefore, represent the 'normal' response in browsed acacias.

Acacia etbaica floral resources did not vary much under different browsing levels, either in flower number (with some decrease in normally browsed trees but less effect under artificial heavy browsing) or in flower size (with a small but significant small increase in floral diameter). It was observed that by the time these trees were

flowering, almost all the leaves were already shed, thereby leaving nothing for browsers, and perhaps allowing resources to be diverted to the flowers. Another difference for this species is that the trees produce flowers all along the branch and not at the leaf nodes as in other *Acacia* species, so that browsing will often leave some developing buds intact. Furthermore, although *Acacia* thorns may be straight or hooked depending upon the species, they are usually capable of keeping all but the largest browsers at bay, though interestingly, straight thorns have been shown to pose little deterrent to impala, while the much smaller hooked thorns, like the ones in *A. etbaica,* succeed in keeping them at bay (Willmer *et. al*., 1999). Impalas are among the commonest browsers of the Ewaso ecosystem including the study area, therefore, it appears *A. etbaica* are probably less severely browsed than other sympatric acacias.

4.2 FLORET AND ANTHER PRODUCTION

a) Florets per inflorescence.

It is clear that browsing affects the number of florets produced in each inflorescence of *Acacia* trees. This was especially true for *A. nilotica* trees, and perhaps this relates to the smaller diameters that were recorded for these flowers. The other *Acacia* species do not seem to vary their floret production so much under different browsing levels, the only major difference being a reduced floret number for heavily browsed *A. brevispica*. This could be due to differences in the growth strategies of these species, possibly lying within their genetic make-up. Whereas *A. brevispica* seems to respond more to normal herbivory by varying its floral production per tree, *A. nilotica* seems to respond more by reducing the number of florets in its inflorescences and hence its inflorescence size. It might be proposed that this difference could pay off

more in favour of *A. nilotica* than *A. brevispica* because browsed trees of the former would still provide high flower number and overall floral display at a distance (and hence more powerful visual attraction to pollinators) than browsed trees of the latter, even if less scent is produced overall in the somewhat thinned *A. nilotica* inflorescences. It has been found that most insect pollinators are initially attracted to flowers by vision rather than by smell (Bernhardt and Walker, 1984; Stone *et al.,* 2003). However, there could also be a disadvantage to this strategy. Reduced production of florets in *A. nilotica* would mean less rewarding flowers, and this might lead to a reduction in pollinator visits, especially in the face of other more highly rewarding plants in neighbouring patches. Plant patches with a high density of flowers will lower the travel costs that a pollinator faces, so that the forager stays in the patch longer and visits more flowers (Rathcke 1983). Hence, if browsing were not controlled (by limiting the number of browsers per habitat patch), then the reproductive potential and success of *A. nilotica* with limited distribution in savannas could be at risk. However, it should also be mentioned that *A. nilotica* normally has the densest and most 'showy' floral display (more inflorescences per branch, and far more florets per inflorescence) than the other two species tested here, so it can perhaps afford to reduce floret production when stressed by herbivory more than is the case for the other species.

It is noteworthy that *A. etbaica*, again, does not seem to vary its floret production per inflorescence in the face of browsing. These results may indicate that the trees are predictably browsed and have a well-developed compensatory growth, aided by the fact that flowering is separated temporally from the time of growth of other tissues including leaves (Karban and Baldwin, 1997; Agrawal, 1998; Gaad *et al.,* 2001). The

hooked thorns could also be effective in reducing herbivory to levels where full compensation is possible. However, this needs more investigation before any conclusions can be made on the effectiveness of deterrent thorns in controlling herbivores.

b) Anthers per floret.

Anther production is perhaps controlled mainly genetically, and it appears that herbivory does not affect its number very greatly in two of the *Acacia* species (*A. nilotica* and *A. brevispica*) investigated. However, there were highly significant increases in anther number per floret in browsed *A. etbaica*, as compared with the small decreases in the other two species (*A. nilotica* and *A. brevispica*). This again may relate to good compensatory growth.

In cases where fewer florets are produced per inflorescence, the anthers produced per inflorescence would also normally be correspondingly fewer and this reduction in pollen resource might affect the number of pollinators attracted to the flowers. *A. etbaica* is the only species that compensates for this effect by increasing the anthers per floret.

In summary, the following effects occur with browsing:

A nilotica: Little change in inflorescence number, decreased inflorescence diameter, decreased florets per inflorescence, unchanged anther number. Net effect: maintained floral display but substantially decreased pollen availability overall.

A. brevispica: Substantial reduction in inflorescence number, some decrease in

diameter, little change in floret or anther number.

Net effect: reduced floral display and reduced overall pollen

availability.

A etbaica: Little change in inflorescence number, some increase in diameter,

some increase in floret number, marked increase in anther number.

Net effect: maintained floral display and possibly increased pollen

availability.

4.3 FLOWER VISITATION AND POLLINATOR DIVERSITY

The effects of reduced flower numbers per tree and/or reduced inflorescence

diameters and/or reduced pollen availability should be reflected in the total number

of pollinators attracted to the flowers. Generally the unbrowsed trees, especially *A.

nilotica* and *A. brevispica* recruited significantly higher number of pollinators than

naturally and heavily browsed trees. In *A. etbaica* however, the browsed trees did

not suffer any reduction in pollinator visit number. These differences might suggest

that both floral display and resource have an effect on attracting pollinators to the

flowers.

Floral display effects could of course simply be mediated by pollinator vision and

olfaction. For example, unbrowsed *A. nilotica* trees would attract more pollinators

(especially bees) than browsed trees because the unbrowsed trees had slightly more

inflorescences per tree and relatively larger inflorescences, thereby becoming more

visible to pollinators from a distance. A similar explanation can be extended to the

trend in results of *A. brevispica* flower pollinator visitation. It is widely recognized

that a plant which has dense flower heads provides a powerful visual and olfactory

cue to pollinators and therefore, attracts more pollinators than those with patchy and sparse flower heads (Rathcke, 1983). Specifically relevant results were recorded by Willmer and Stone (1997) in Tanzania, showing that larger bee species such as *Xylocopa* and *Apis mellifera* only visited *Acacia* species with dense, flower-rich heads while avoiding those with very sparse flower heads.

Resource effects may be mediated by pollen uptake rate and also influenced by experience and memory in bees. Rathcke (1983) reported that while many pollinators are driven by the quantity and quality of the resources, a plant's reproductive success is limited by pollinator activity so that individual plants compete for effective pollen carriers. Evidence exists that bee pollinators recognize and learn about high rewarding plants, and may associate nectar and pollen rewards with floral cues such as color and size, perhaps even being able to remotely see and smell the nectar (reviewed by Willmer and Stone, 2004).

Overall, the differences in visitation frequencies in effect mean that less browsed *Acacia* trees are likely to be more reproductively fit than heavily browsed trees, and that unbrowsed trees are likely to be the most reproductively fit and therefore, stand a better chance of survival should resources in the environment become limiting. Only *Acacia etbaica* seems to be able to limit these deleterious effects of browsing, and it may therefore, be the best able to cope with heavy browsing levels.

There are also more subtle effects of varying floral resources due to differential herbivory, however, which can be seen in the patterns of pollinator visitation across the day. Unbrowsed trees reached an earlier pollinator peak activity than browsed

trees of *A. nilotica, A. brevispica* and *A. etbaica,* with bees in each case being mainly responsible for the shift. It is possible that flowers must reach a certain threshold of scent emission in order to recruit maximum pollinators. Where the scent comes directly from the floral tissues, this threshold could be 'automatically' linked to the flowers' nutritive value and quantity of reward, as suggested by Bernhardt and Walker (1984). From the results shown in Figs 3a, 4a and 5a, it seems that browsing indeed causes a shift in peak pollinator activity, delaying the peak by at least 2 hours and sometimes up to 6 hours. Thus, browsing may be affecting the release of strong, species-specific scents that may provide a synchronizing cue announcing the availability of a fresh standing crop of flowers (pollen) in each tree, detectable by the solitary and social bees which are the main pollen carriers (Willmer and Stone, 1997). As a result, unbrowsed tree flowers are more detectable, and reach peak pollinator activity, earlier than browsed trees. The browsing-associated changes in scent density would be expected to delay particular more specific types of visitors (e.g. bees) picking up the cue, while having little effect on non-specific visitors, in accordance with what was observed.

An alternative (though not mutually exclusive) explanation of temporal pollinator shifts would be that browsing-induced changes in the numbers or sizes of flowers (as summarized above) would make the plant less attractive overall (visually, scent-wise or even in terms of overall rewards). This could make the plant not visited until after the adjacent unbrowsed more floriferous or more rewarding trees have been thoroughly visited and had their rewards depleted, i.e. browsed plants are only attractive to pollinators after nearby unbrowsed trees have been visited and depleted. A corollary of this might even be that browsed trees could tend to adaptively shift

their resources to attract pollinators later in the day, after the unbrowsed trees have been pollinated, such that they avoid competition for a limited pool of pollinators. This would be a further survival strategy to compensate for herbivory.

The foregoing observations may explain the fact that more pollinators were recorded inside the enclosure (on unbrowsed trees) than outside. More flowers occurred within the enclosure, with plenty of unbrowsed trees that probably attracted more pollinators because they would be more rewarding. The main visitor recorded inside the enclosure was the honeybee, which seem to be the most important pollinator; but for nearly all the pollinators (apart from wasps) recorded visiting the trees under investigation, there was generally a higher number inside the enclosure than outside.

4.4   PATTERNS OF POLLEN RELEASE AND TIMING

Pollinator activity on unbrowsed *A. nilotica* trees synchronized almost perfectly with patterns of dehiscence of flowers and pollen release, all peaking around 1000hr. This synchrony is to be expected for various reasons: the scent produced by the dehiscing flowers would provide a powerful olfactory attractant, coupled with the bright color of dehisced flower heads, which would visually attract the visitors, and of course the pollinators will have learnt to associate such cues with the amount of reward that they would gain from the plant (Stone *et al.,* 2003).

However, naturally browsed *A. nilotica* trees reached their peak flower dehiscence around the same time as unbrowsed trees, whereas peak visitation of pollinators to these browsed trees occurred later on in the day; in other words, pollen availability and visitation seem to be uncoupled. This suggests that the browsed trees are indeed

suffering from competition with unbrowsed conspecifics, and it may indicate that they cannot alter the time of dehiscence to regulate peak pollinator activity and avoid competition with unbrowsed or less browsed trees within the vicinity.

For *Acacia brevispica,* there was again a reasonably good temporal match between pollen presentation and visitor frequency for unbrowsed trees. Here the browsed trees again showed a shift in pollen presentation to later in the day (around 15h00) that was matched (with some delay) by a shift in visitor peak to around 16h00-17h00.

For *Acacia etbaica*, the sharp peak in pollen presentation in unbrowsed trees was almost entirely lost in browsed trees, where the flowers instead seemed to dehisce more gradually through the day. Nevertheless the visitor peak still moved to later in the day, and was not particularly well synchronized with pollen availability even in the unbrowsed trees. This might suggest that the shift in visitor peaks is more related to competition from unbrowsed trees than to any direct cue from the tree or its flowers.

Why do changes and shifts in pollen presentation occur in browsed trees? One possibility is that there is modification of microclimate around the flowers that makes the flowers open later in the day. The browsed trees tend to have lots of fine branches and dense new small foliage around the flowers which changes the microclimate thereby making the air around the flowers more humid so they dehisce a bit later than the unbrowsed trees (Stone *et al.,* 1998).

4.5   WILD FLOWER DIVERSITY

The higher species numbers of wild plants bearing flowers recorded outside the enclosure than inside could be attributed to introduction by herbivores. Herbivore feeding provides a channel of seed dispersal and therefore, could be responsible for dispersing the seeds and propagules of wild plants across habitat as they forage (Coughenour, 1985; O'Connor and Roux, 1995; Fahnestock and Detling, 1999). Exclusion of herbivores limits herbivore dispersal and therefore, plants would mainly rely on wind pollination or other forms of dispersal independent of herbivores.

However, the influence of the flowers of other wild plants in recruiting pollinators that would in turn visit *Acacia* flowers does not seem significant. The reason could be that most of the wild flowers present nectar rewards to pollinators unlike the acacias investigated that present pollen rewards. The wild flowers would therefore, mostly recruit nectar feeders whereas the acacias investigated recruited mostly pollen feeders, particularly bees. However, it would be expected that availability of nectar in nearby herbs would still be an attractant to solitary bees at least, since these often collect both resources on a single foraging trip.

CHAPTER 5

CONCLUSION AND RECOMMENDATION

5.1 CONCLUSION

a) It is clear that herbivores can have significant negative effects on the interplay between pollinators and flowers of *Acacia*. Particular effects seem to be on *A. nilotica* and *A. brevispica* where herbivore exclusion is associated with increase in flower size and/or numbers on trees. This increase brings about an increase in the number of pollinators that visit their flowers. In general the unbrowsed trees, especially *A. nilotica* and *A. brevispica,* recruited significantly higher numbers of pollinators than naturally and heavily browsed trees, which could be a composite effect of vision and olfaction together with resource (pollen) availability. The unbrowsed trees had more inflorescences produced per tree and relatively larger flowers, thereby becoming more visible to pollinators from a distance than those of browsed trees.

b) Unbrowsed trees also reached an earlier pollinator peak activity than browsed trees of *A. nilotica, A. brevispica* and *A. etbaica.* This may suggest that flowers need to reach a certain threshold of scent in order to recruit maximum pollinators. However it is also possible that unbrowsed trees simply compete better for pollinators early in the day (e.g. due to their better visual display or higher pollen reward) and browsed trees are only visited later on when the intact trees have been depleted.

c) A general delay in dehiscence of browsed trees was recorded which may possibly have been caused by modification of the microclimate around the flowers making them open later in the day than unbrowsed trees.

d) This study has shown that *A. nilotica* and *A. brevispica* vary their floral resources greatly when browsed, whereas *A. etbaica* tends to show compensatory floral growth. It is not known, however, how herbivory affects any of these trees' reproductive ecology on wider spatial and temporal scales. A study needs to be done to establish whether plants recover later on in the year from herbivory. Sampling from varied geographical localities also needs to be done to establish if there is any spatial variation in effects of herbivory on pollinator dynamics and floral attributes of these trees.

e) Ecologically, the 3 tree species investigated here are extremely important by acting as pollinator reservoirs in supporting a large pool of pollinators, since the trees flower sporadically in most parts of the year, unlike most other *Acacia* spp. and unlike most herbs that grow in savanna communities. Bees, which are very crucial in the reproductive ecology of most plants, are the common pollinators of these trees. Furthermore, most herbivores prefer these trees to other species because they are easy to nibble (especially *A. nilotica*). The trees also lack ant guards, as found in *A. drepanolobium*, making them more vulnerable to herbivore attack.

5.2   RECOMMENDATIONS

Herbivory seems to perform an important role in the reproductive ecology of Acacias, especially *A. nilotica* and *A. brevispica*. More specific studies therefore, need to be done on the following areas to confirm these results:

i.   Over a large geographical area with variations in edaphic and environmental factors to determine the spatial variation in the effect of herbivory on floral resource variation and pollinator-plant interactions.

ii. Over several growth seasons to establish the temporal variations of the effect of herbivores on the interactions between flowers and pollinators of different *Acacia* species.

iii. On other *Acacia* species apart from the three in this study to establish the range of *Acacia* species affected by herbivory. Work on species with tight flowering seasons would be especially useful.

iv. To establish the effect of wildlife and livestock herbivory on *Acacia* floral attributes and community-level pollinator dynamics in Kenya, to highlight the sensitive pollinator species that may be at risk following herbivory.

REFERENCES

Agrawal, A. A. (1998). Induced responses to herbivory and increased plant performance. Science **279**: 1201–1202.

Armbruster, W. S. (1984). The role of resin in angiosperm pollination: ecological and chemical considerations. American Journal of Botany **71**: 1149-1160.

Armbruster, W.S. and Herzig, A.L. (1984). Partitioning and sharing of pollinators by four sympatric species of *Dalechampia* (Euphorbiaceae) in Panama. Annals of the Missouri Botanical Garden **71**:1-16.

Barth, F. G. (1985). 'Insects and Flowers: the Biology of a Partnership'. Princeton University Press, Princeton, New Jersey.

Bawa, K.S. and Hadley, M. (1990). 'Reproductive Ecology of Tropical Forest Plants'. Parthenon Publishing Group.

Beentje, H. (1994). 'Kenyan trees shrubs and lianas.' National Museums of Kenya: Nairobi, Kenya.

Belsky, A. J. (1994). Influences of trees on savanna productivity: tests of shade, nutrients, and tree-grass competition. Ecology **75:** 922–932.

Bernhardt, P. and Walker, K. (1984). Bee foraging on three sympatric species of Australian *Acacia.* International Journal of Entomology **26**: 322-330.

Brain, P. (1987). Immunology and phylogeny: a preliminary study of *Acacia.* South African Journal of Science **83**: 422-427.

Buchmann, S.L. and Cane, J.H. (1989). Bees assess pollen returns while sonicating *Solanum* flowers. Oecologia **81**: 289-294.

Clay, K. (1988). Fungal endophytes of grasses: a defensive mutualism between plants and fungi. Ecology **69**: 10-16.

Coe, M. & Beentje, H. (1991). 'A Field Guide to the Acacias of Kenya'. Oxford University Press, Oxford.

Coe, M. & Coe, C. (1987). Large herbivores, Acacia trees and bruchid beetles. South African Journal of Science **83**: 624-635.

Conner, J.K. and Rush, S. (1996). Effects of flower size and number on pollinator visitation to wild radish, *Raphanus raphanistrum*. Oecologia **105**: 509–516.

Coughenour, M.B. (1985). Graminoid responses to grazing by large herbivores: adaptations, expectations and interacting processes. Annual Missouri Botanic Garden **72**:852-853.

Crawley, M. J. (1983). 'Herbivory: the dynamics of animal-plant interactions'. Studies in Ecology, Volume 10. Univ. of California Press.

Cunningham, S. A. (1995). Ecological constraints on fruit initiation by *Calyptrogyne ghiesbreghtiana* (Arecaceae): floral herbivory, pollen availability, and visitation by pollinating bats. American Journal of Botany **82**:1527-1536.

Davenport, T.L. (1982). Avocado growth and development. Proceedings of the Florida State Horticultural Society **95**: 92-96.

Dressler, R.L. (1982). Biology of the orchid bees (Euglossini). Annual Review of Ecology & Systematics **13:**373-394.

Dublin, H. T. (1995). Vegetation dynamics in the Serengeti-Mara ecosystem: the role of elephants, fire, and other factors. In: 'Serengeti II: dynamics, management, and conservation of an ecosystem'. (ed Sinclair, A. R. E. and Arcese, P.), pp. 71–90. Univ. of Chicago Press.

Eltz, T., Whitten, W.M., Roubik, D.W., and Linsenmair, K.E. (1999). Fragrance collection, storage and accumulation by individual male bees. Journal of Chemical Ecology **25**:157-176.

Faegri, K. and van der Pijl, L. (1979). 'The Principles of Pollination Ecology'. Pergamon Press, Oxford.

Fahnestock, J.T. and Detling, J.K. (1999). The influence of herbivory on plant cover and species composition in the pryor Mountain Wild Horse Range, USA. Plant Ecology **144**: 145-157.

Frankie, G.W., Haber, W.A., Opler.P.A. and Bawa K.S. (1983). Characteristics and organization of the large bee pollination system in the Costa Rican dry forest. In 'Pollination Biology' (ed. L. Real) pp 411-447. Academic Press, New York, USA.

Frazee, J. and Marquis, R. (1994). Environmental contribution to floral trait variation in *Chamaecrista fasciculata* (Fabaceae: Caesalpinaceae). American Journal of Botany **81**: 206-215.

Gaad, M.E., Young, T.P. and Palmer T.M. (2001). Effects of simulated shoot and leaf herbivory on vegetative growth and plant defense in *Acacia drepanolobium.* Oikos **92**: 515-521.

Galen, C. (1989). Measuring pollinator-mediated selection on morphometric floral traits: bumblebees and the alpine sky pilot, *Polemonium viscosum*. Evolution **43**:882-890.

Gilbert, F.S. (1981). Foraging ecology of hoverflies: morphology of mouthparts in relation to feeding on nectar and pollen in some common urban species. Ecological Entomology **6:** 245-262.

Grant, S. (1984). 'Beauty and the beast'. p 1-13. Charles Scribner& Sons, New York.

Grubb, P. J. (1986). Sclerophylls, pachyphylls, and pycnophylls: The nature and significance of hard leaf surfaces. In: 'Insects and the Plant Surface'. (ed B.E. Juniper and T.R.E. Southwood) pp. 137-150. Edward Arnold, London.

Hay, M. E. (1986). Associational plant defenses and the maintenance of species diversity: turning competitors into accomplices. American Naturalist **128**:617-641.

Hay, M. E. and W. Fenical (1988). Marine plant-herbivore interactions: The ecology of chemical defense. Annual Review of Ecology & Systematics **19**: 111-145.

Heithaus, E. R., Stashko, E. and Anderson, P.K. (1982). Cumulative effects of plant-animal interactions on seed production by *Bauhinia ungulata*, a neotropical legume. Ecology **63**:1294-1302.

Herrera, C. M. (1989). Vertebrate frugivores and their interaction with invertebrate fruit predators: supporting evidence from a Costa Rican dry forest. Oikos **54**:185-188.

Herrera, C. M. (1993). Selection on floral morphology and environmental determinants of fecundity in a hawk moth pollinated violet. Ecological Monographs **63**:251-275.

Herrera, C.M. (2000). Measuring the effects of pollinators and herbivores: Evidence for non-additivity in a perennial herb. Ecology **81**: 2170–2176.

Howe, H. F. and L. C. Westley (1988). 'Ecological Relationships of Plants and Animals'. Oxford University Press, New York.

Hulme, P. E. (1996). Herbivores and the performance of grassland plants: a comparison of arthropod, mollusc and rodent herbivory. Journal of Ecology **84**: 43–51.

Janzen, D. H. (1966). Coevolution of mutualism between ants and acacias in Central America. Evolution **20**: 249-275.

Janzen, D. H. (1974). Swollen thorn acacias of Central America. Smithsonian Contributions to Botany **13:** 1-131.

Karban, R. and Baldwin, I. T. (1997). 'Induced Responses to Herbivory'. Univ. Chicago Press.

Keesing, F. (1998). Impacts of ungulates on the demography and diversity of small mammals in central Kenya. Oecologia **116**: 381–389.

Kenrick, J. (2003). Review of pollen-pistil interactions and their relevance to reproductive biology of *Acacia*. Australian Systematic Botany **16**: 119-130.

Kenrick, J. and Knox, R.B. (1982). Function of polyads in reproduction of *Acacia*. Annals of Botany **50**: 721-727.

Kimsey, L.S. (1980). The behavior of male orchid bees (Apidae, Hymenoptera, Insecta) and the question of leks. Animal Behaviour **28**: 996-1004.

Krebs, C.J. (1989). 'Ecological Methodology'. Harper Collins.

Krüger, O. and McGavin, G.C. (1998). The insect fauna of *Acacia* species in Mkomazi Game Reserve, North East Tanzania. Ecological Entomology **22**: 440-444.

Le Houerou, H.N. (1980). Chemical composition and nutritional value of browse in tropical West Africa. In: 'Browse in Africa, the Current State of Knowledge'. (ed Le Houerou, H.N.), pp 261-289. ILCA, Ethiopia.

Lehtila K., and Strauss, S.Y. (1997). Leaf damage by herbivores affects attractiveness to pollinators in wild radish, *Raphanus raphanistrum*. Oecologia **111**: 396-403.

Lehtila, K. and. Strauss, S. (1999). Effects of foliar herbivory on male and female reproductive traits of wild radish, *Raphanus raphanistrum*. Ecology **80**: 116-124.

Levin, D.A and Anderson, W.W. (1970). Competition for pollinators between simultaneously flowering species. American Naturalist **104**: 455-467.
Levin, D. A. (1973). The role of trichomes in plant defense. Quarterly Review of Biology **48**: 3-15.

Marquis, R. J. and C. J. Whelan (1994). Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. Ecology **75**: 2007-2014.

Marquis, R. (1992). A bite is a bite is a bite? Constraints on response to folivory in *Piper arieianum* (Piperaceae). Ecology **73:** 143-152.

McNaughton, S.J. (1983). Compensatory plant growth as a response to herbivory. Oikos **40:** 329-336.

McCall, C. and Primack, R.B. (1992). Influence of flower characteristics, weather, time of day, and season on insect visitation rates in three plant communities. American Journal of Botany **79:** 434-442.

Michener, C.D. (2000). 'The Bees of the World'. The Johns Hopkins University Press, Baltimore.

Midgely, S.J. and Turnbull, J.W. (2003). Domestication and use of Australian acacias: case studies of five important species. Australian Systematic Botany **16**: 89-102.

Milewski, A. V., Young, T. P. and Madden, D. (1991). Thorns as induced defenses: Experimental evidence. Oecologia **86**: 70–75.

Miller, M.F. (1995). Acacia seed survival, seed germination and seedling growth following pod consumption by large herbivores and seed chewing by rodents. African Journal of Ecology **33**: 194-210.

Milton, S.J. and Moll, E.J. (1982). Phenology of Australian Acacias in the SW Cape, South Africa, and its implications for management. Botanical Journal of the Linnean Society **84**: 295-327.

Morgan, A., Carthew, S.M. and Sedgley, M. (2002). Breeding System, Reproductive efficiency and weed potential of *Acacia baileyana.* Australian Journal of Botany **50**: 398-402.

Murawski, D. A. (1987). Floral resource variation, pollinator response, and potential pollen flow in *Psiguria warscewiczii*. Ecology **68**:1273-1282.

Mutikainen, P. and Delph, L. (1996). Effects of herbivory on male reproductive success in plants. Oikos **75**: 353-358.

O'connor, T.G. and Roux, P.W. (1995). Vegetation changes (1949-71) in a semi arid, grassy dwarf shrubland in the Karoo, South Africa: influence of rainfall variability and grazing by sheep. Journal of Applied Ecology **32**: 612-626.

Ollerton, J and Lack, A.J. (1992). Flowering phenology: an example of relaxation of natural selection? Trends in Ecology and Evolution **7**: 274-276.

Ostfeld, R. S. and Canham, C. D. (1993). Effects of meadow vole population density on tree seedling survival in old fields. Ecology **74**: 1792–1801.

Ostfeld, R. S., Manson, R. H. and Canham, C. D. (1997). Effects of rodents on survival of tree seeds and seedlings invading old fields. Ecology **78**: 1531–1542.

Palmer, T.M. and Young, T.P. (2000). Short-term dynamics of an acacia ant community in Laikipia, Kenya. Oecologia **123**: 425-435.

Paynter, Q., Csurhes, S.M., Heard, T.A., Irseson, J., Julien, M.H., Lloyd, J., Lonsdale, W.M., Palmer, W.A., Sheppard, A.W., and van Klinken, R.D. (2003). Worth the risk? Introduction of legumes can cause more harm than good: an Australian perspective. Australian Systematic Botany **16**: 81-88.

Pellew, R. A. P. (1983). The impact of elephant, giraffe and fire upon the *Acacia tortilis* woodlands of the Serengeti. African Journal of Ecology **21**: 41–78.

Quesada, M., Bollman, K. and Stephenson, A. (1995). Leaf damage decreases pollen production and hinders pollen performance in *Cucurbita texana*. Ecology 76: 437-443.

Raine, N. E. (2001). The pollination ecology of a Mexican *Acacia* community. Ph.D. Dissertation. University of Oxford, Oxford, UK.

Raju, S.A.J. and Rao, S.P. (2002). Pollination ecology and fruiting behaviour in *Acacia sinuata* (Lour.)Merr. (Mimosaceae), a valuable non-timber forest plant species. Current Science 82:1466-1471.

Rathcke, B. (1983). Competition and facilitation among plants for pollination. In: 'Pollination Biology' (ed L. Real), pp 305-329. Academic Press, New York.

Rathcke, B. (1988). Flowering phonologies in a shrub community: competition and constraints. Journal of Ecology **76**: 975-994.

Rausher, M. D. and Simms, E. L. (1989). The evolution of resistance to herbivory in *Ipomoea purpurea*. I. Attempting to detect selection. Evolution **43**: 563–572.

Regino, Z. (2000). Functional equivalence in plant-animal interactions: ecological and evolutionary consequences. Oikos **88**: 442-447.

Rohner, C. & Ward, D. (1999). Large mammalian herbivores and the conservation of arid Acacia stands in the Middle East. Conservation Biology **13:** 1162-1171.

Rosenthal, G. A. and M. R. Berenbaum. (1992). 'Herbivores: their interactions with secondary plant metabolites. Vol. II: Evolutionary and ecological processes'. Academic Press, New York.

Rosenthal, G. A. and D. H. Janzen. (1979). 'Herbivores: their interaction with secondary plant metabolites'. Academic Press, New York.

Ross, J.H. (1981). An analysis of the African *Acacia* species: their distribution, possible origins and relationships. Bothalia **13**: 389-413.

Roubik, D.W. (1989). 'Ecology and Natural History of Tropical Bees'. Cambridge University Press, Massachusetts, USA.

Roubik, D.W. (1998). Grave-robbing by male *Eulaema* (Hymneoptera, Apidae): Implications for euglossine biology. Journal of the Kansas Entomological Society **71**: 188-191.

Schemske, D. W. and Horvitz, C.C. (1988.) Plant-animal interactions and fruit production in a neotropical herb: a path analysis. Ecology **69**: 1128-1137.

Sedgely, M., Harbbard, J., Smith, R-M.M. Wickneswari, R. and Griffin, A.R. (1992). Reproductive biology and interspecific hybridisation of *Acacia mangium* and *Acacia auriculiformis* A. Cunn. Ex Benth. (Leguminosae: Mimosaceae). Australian Journal of Botany **40**: 37-48.

Shaw, M.T., Keesing, F. and Ostefeld R. S. (2002). Herbivory on *Acacia* seedlings in East African Savanna. Oikos **98:** 385-392.

Sinclair, A. R. E. (1995). Equilibria in plant-herbivore interactions. In: Serengeti II: Dynamics, management, and conservation of an ecosystem. (ed Sinclair, A. R. E. and Arcese, P.), pp. 91–113.Univ. of Chicago Press.

Stone, G.N., Willmer, P.G. and Nee, S. (1996). Daily partitioning of pollinators in an *Acacia* community. Proceedings of the Royal Society B, **263**: 1389-1393.

Stone, G.N., Willmer, P.G., and Rowe, J.A. (1998). Partitioning of pollinators during flowering in an African *Acacia* community. Ecology **79:** 2808-2827.

Stone, G.N., Raine, N.E., Prescott, M. and Willmer, P.G. (2003). Pollination ecology of Acacias (Fabaceae, Mimosoideae). Australian Systematic Botany **16**: 103-118.

Strauss, S. Y. (1997). Floral characters link herbivores, pollinators, and plant fitness. Ecology **78**: 1640-1645.

Strauss, S. Y. and Agrawal, A. A. (1999). The ecology and evolution of plant tolerance to herbivory. Trends in Ecology & Evolution **14**: 179–185.

Strauss, S. Y., Conner, J. and Rush, S. (1996). Foliar herbivory affects floral characters and plant attractiveness to pollinators: implications for male and female fitness. American Naturalist **147**: 1098-1107.

Tandon, R. Shivanna, K.*R.* and Mohan Ram, H.Y. (2001). Pollination biology and breeding system of *Acacia senegal*. Botanical Journal of the Linnaean Society **135**: 251-262.

Townsend, J. (2002). Practical statistics for environmental and biological scientists, John Wiley and sons, West Sussex.

Turnbull, J.W. (1987) (Ed.) 'Australian acacias in developing countries.' Australian Centre for International Agricultural Research Proceedings **16** Canberra, Australia.

Tybirk, K. (1989). Flowering, pollination and seed production of *Acacia nilotica*. Nordic Journal of Botany **9**: 375-381.

Tybirk, K. (1993). Pollination breeding system and seed abortion in some African *Acacia* species. Botanic Journal of the Linnaean Society **112**: 107-137.

Willmer P. G. and Stone, G.N. (1997). How aggressive ant-guards assist seed-set in *Acacia* flowers Nature **388:** 165 -167.

Willmer, P.G., Stone, G.N and Mafunde, D. (1999). Ants, pollinators and Acacias in Mkomazi. In: 'Mkomazi; the ecology, biodiversity and conservation of a Tanzanian savanna', (ed Coe, M.), pp 361-370. Royal Geographical Society, London.

Willmer, P.G. & Stone, G.N. (2004). Behavioural, ecological and physiological determinants of the activity patterns of bees. Advances in the Study of Behavior. In press.

Young, T. P., Stubblefield, C. H. and Isbell, L. A. (1997). Ants on swollen-thorn acacias: Species coexistence in a simple system. Oecologia **109**: 98–107.

Young, T. P. and Isbell, L. A. (1991). Sex differences in giraffe feeding ecology:energetic and social constraints. Ethology **87**: 79–89.

Young, T. P. and Okello, B. D. (1998). Relaxation of an induced defense after exclusion of herbivores: spines on *Acacia drepanolobium*. Oecologia **115**: 508–513.

Young, T. P., Okello, B. D., Kinyua, D. and Palmer, T. M. (1998). KLEE: a long-term multi-species herbivore exclusion experiment in Laikipia, Kenya. African Journal of Range & Forage Science **14**: 94–102.

APPENDICES

Appendix 1: Mean daily visitation of *Acacia* spp. under different browsing levels.

A. nilotica	POLLINATOR	TIME									
		08h00-09h00	09h00-10h00	10h00-11h00	11h00-12h00	12-h00-13h00	13h00-14h00	14h00-15h00	15h00-16h00	16h00-17h00	17h00-18h00
Unbrowsed	BEE	0	13	27	22	19	10	7	0	1	0
	FLIES	0	3	6	2	2	1	0	0	0	1
	BEETLE	0	0	3	0	0	2	1	0	0	0
	WASP	0	0	5	0	1	2	0	0	0	0
	OTHER	1	0	2	1	1	1	0	1	0	0
	TOTAL	1	16	43	25	23	16	8	1	1	1
Browsed	BEE	1	1	3	3	7	5	3	0	2	1
	FLIES	1	1	1	0	0	0	0	2	0	0
	BEETLE	0	0	0	0	3	2	1	1	1	0
	WASP	0	0	0	0	0	0	0	0	0	0
	OTHER	1	1	0	0	0	0	1	0	0	0
	TOTAL	3	3	4	3	10	7	5	3	3	1
A. brevispica											
Unbrowsed	BEE	1	17	20	18	7	3	3	2	0	0
	FLIES	19	10	15	8	3	1	0	1	0	1
	BEETLE	0	1	3	1	0	1	1	1	0	0
	WASP	0	0	0	0	0	0	0	1	1	0
	OTHER	0	0	2	1	0	0	2	0	0	0
	TOTAL	20	28	40	28	10	5	6	5	1	1
Browsed	BEE	1	2	2	3	3	2	4	6	7	3
	FLIES	5	3	2	2	4	2	1	3	5	0
	BEETLE	0	0	1	0	0	0	0	0	1	0
	WASP	0	0	0	0	0	0	0	0	0	0
	OTHER	0	0	1	2	0	0	0	1	0	0
	TOTAL	6	5	6	7	7	4	5	10	13	3
A. etbaica											
Unbrowsed	BEE	3	2	5	3	2	1	8	3	1	0
	FLIES	0	1	2	0	0	1	0	0	0	0
	BEETLE	0	0	1	1	0	0	1	0	0	0
	WASP	0	0	3	1	0	0	0	0	0	0
	OTHER	0	0	3	2	1	3	0	0	0	0
	TOTAL	3	3	14	7	3	5	9	3	1	0
Browsed	BEE	2	3	1	6	4	1	0	0	1	0
	FLIES	0	0	0	2	5	0	0	0	0	1
	BEETLE	0	3	0	1	4	0	0	0	0	0
	WASP	0	1	3	1	0	0	0	0	0	0
	OTHER	0	0	0	0	0	0	0	0	0	0
	TOTAL	2	7	4	10	13	1	0	0	1	1
Heavy browsed	BEE	0	2	3	2	3	3	5	2	1	0
	FLIES	0	1	2	1	2	3	2	1	0	0
	BEETLE	0	0	0	1	1	2	3	1	1	0
	WASP	0	0	0	1	2	3	4	2	1	0
	OTHER	0	0	0	1	2	1	3	1	0	0
	TOTAL	0	3	5	6	10	12	17	7	3	0

Appendix 2: Families of insect pollinators recorded inside and outside enclosure.

Family	No. inside	No. outside
Apidae	154	118
Ascilidae	2	
Bombyliidae	3	1
Braconidae		1
Calliphoridae	24	7
Cerambycidae	8	5
Chrysomelidae	17	4
Coccinelidae	1	
Elateridae	1	2
Eumenidae	3	2
Halictidae	14	8
Icnenumonidae	2	2
Lycaenidae	4	1
Lycidae	4	4
Megachilidae	4	
Meloidae	12	12
Melyridae		3
Muscidae	23	6
Nymphalidae	2	
Pompilidae		1
Pyrrhochoridae	8	3
Sarcophagidae	17	6
Scarabaeidae	6	6
Sesiidae		1
Sphecidae	3	
Syrphidae	3	1
Tachnidae	1	3
Tenebrionidae	15	4
Tiphidae		1

Appendix 3: Common bee species collected inside and outside enclosure.

Family	Species	No. Inside	No. outside
Apidae	*Amegilla*	16	3
	Apis mellifera	105	111
	Plebeird hildebraudti	1	1
	Tetraloniella		1
	Thyreus	4	1
	Xylocopa somalica	8	1
Halictidae	*Lasioglossum*	1	1
	Lipotriches	14	5
	Patellapis	2	2
	Patellapis		2
Megachilida	*Megachile*	3	
	sp. 1	1	

Appendix 4: Wild plant species diversity inside and outside enclosure

Speceis	Wild plant species diversity	
	no. inside	no. outside
Abutilon grandiflorum	21	92
Barleria ramulosa		31
Bidens sp.	2	39
Commelina africana	17	4
Commelina forskalei	12	53
Commelina latifolia	3	9
Commelina sp.	4	59
Craterostigma sp.		1
Gutenbergia cordifolia	2	11
Helichrysum glumaceum		8
Hibiscus flavifolius		6
Hypoestes sp.		257
Indigofera volkensii	15	25
Justicia sp.	9	
Kalanchoe densifolia	4	87
Kalanchoe schewinfurthii	2121	6
Lippia sp.	6	2
Melhania angustifolia	24	11
Melhania ovata		1
Ocimum handience	4	231
Pavonia gallaensis	67	189
Pentanisia ouranogyne		2
Plectranthus caninus	64	156
Portulaca quadrifida	24	107
Saccostema sp.	21	3
Sida cordiflolia	1	
Solanum incanum	215	103
Spp A	10	
Spp B		26
Total	**2646**	**1519**