TITLE

THE COMPLIMENTARY ROLE OF WILD HABITATS IN CROP POLLINATION: A CASE STUDY ON THE EGGPLANT (*Solanum melongena* L., Solanaceae)

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DECLARATION

I, Alfred Ochieng' Oluoch, hereby declare that this thesis is my original work and has not been submitted for a degree in any other university.

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Date: 6/7/2001

This thesis has been submitted for examination with our approval as supervisors.

Signed: ______________________

Dr. Barbara Gemmill

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Prof. T. K. Mukiama

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DEDICATION

This work is dedicated to my late parents, Mr. and Mrs. George Oluoch

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ABSTRACT

In this study, carried out in Nguruman, southwestern Kenya, 10 bee species were identified as eggplant pollinators. Their foraging behaviour was shown to be affected by the prevailing ambient temperature and not time of the day or the number of flowers per square meter in the eggplant fields.

Only 2 bee species, *Xylocopa caffra* and *Nomia* sp., visited the eggplant blossoms at a great frequency. Their pollinator effectiveness was determined in two eggplant cultivars (the Black Beauty and the Early Long Purple). *X. caffra* proved to be the most effective pollinator of the eggplant.

Floral manipulations performed to study the most effective mode of pollination in the eggplant revealed that although the eggplant is self-compatible, it needs efficient pollinators for fruit set. Flowers that were hand pollinated with pollen from their own anthers resulted in fruits with high seed set. The eggplant therefore needs an effective mode of pollination to transfer the pollen from the anthers to the stigmas. Seed set in fruits of open-pollinated flowers were higher than in self-pollinated flowers but not as high as in hand-pollinated flowers

Alternative forage resources that the pollinators foraged were also determined. A total of 12 plant species were identified over a five month period along a transect that traversed the surrounding wild habitat. The most preferred alternative flowering plants such as *Duosperma kilimandscharicum*, *Commicarpus helenae* and *Justicia flava* were mainly found in the farm area which was highly foraged throughout the study period. The riparian forest was also highly foraged in some months.

The farm areas and the riparian forest should therefore be maintained because they provide alternative forage and nesting sites for the eggplant pollinators. Fragmentation of the habitat would lead to loss of pollinators and a subsequent reduction in the yield of the eggplant

INTRODUCTION

Importance of pollination

Pollination is a critical and basic ecosystem function, which facilitates biological diversity. It is partly through pollination that plants' genomes are passed on to the next generations. Pollinators transfer pollen from flowers of one plant to those of another of the same species and, as such, are essential for completing the sexual reproductive cycle in zoophilous self-incompatible plants. It is probable that, via entomophily, cross-pollination has been the success of most flowering plants since cross-breeding facilitates heterozygosity in genepools and thus a wide array of genes become available for natural selection.

More than 75% of all flowering plants are entomophilous (Tepedino, 1979) and for them, pollinators are as critical as light and water, since without pollinators, their reproductive success is greatly limited (Levin, 1971). Pollination is a vital link in natural communities connecting plants and animals in key and essential ways (Bond, 1994; Kearns and Inouye, 1997). The pollinators visit the flowers in search of pollen and nectar that they use as food. In addition flowers benefit since, during this process, pollen grains are transferred between the flowers, resulting in cross-pollination. Therefore, pollinators and flowers have a mutually beneficial relationship.

Pollination is a function that is key to man's existence as well. Insect pollinators are essential for many fruits and vegetable crops and the demand for pollinators grows as agricultural productivity grows. Past experience has shown that a single pollinator species should not be relied upon; crops set seeds best with a variety of pollinators that are present under varying seasonal and climatic conditions.

Classification of the Eggplant

The eggplant (*Solanum melongena* L.) belongs to the family Solanaceae. This family has two subfamilies, namely the subfamily Cestroideae and the subfamily Solanoideae. The Cestroidea are mostly found in the Americas and consist of about 18 genera. Most members of this subfamily have narrow flowers, thick seeds, and a wide variety of chromosome numbers. The largest genus in this subfamily is the genus *Cestrum* (D'Arcy, 1979). The subfamily Solanoideae is quite large and has around 80 genera, including the genus *Solanum*, one of the world's largest genera of flowering plants with more than 1000 species. The eggplant belongs to this subfamily and genus (D'Arcy, 1979).

The eggplant was first taken into domestication in southeastern Asia, although it is probable that its seeds might have floated there from Africa, where many similar species are found (D'Arcy, 1979). Arabs took the cultivated forms to Spain and the Persians to Africa. It has now spread throughout the tropics. Two cultivars grown in Kenya, including the area under study are Black Beauty and Early Long Purple.

Economic Importance of the Eggplant

The cooked fruit provides a useful vegetable throughout much of the world. They might be boiled, fried or stuffed. The unripe fruits are sometimes used in curries.

The eggplant is a very important horticultural crop that fetches quite a lot of money for both the farmers and the exporters. In 1997 for instance, the market value for the eggplant export from Kenya was worth 2,075,086.36 US dollars (GTZ annual report, 1998).

There are many factors that can result in the reduction of the eggplant yield, for example nutrition, pests and plant diseases. Considerable work has already been completed on these more traditional links to plant yield; yet pollination, though little studied may be just as important in production. Moreover, losses due to insufficient fertilizer or plant pests are easier to control with agricultural inputs. However, pollinators are a natural service provided by ecosystems. It will be critical to document which pollinators are most effective for the eggplant so that their services are conserved as agricultural areas are developed.

The Study Area

The Nguruman area is in the southwestern part of Kenya. The area of study is comprised of the Ol Kirimatian Maasai group ranch, one of the 51 ranches of Kajiado district of the Rift Valley province, Kenya. The study area is bordered on the western side by the steep Nguruman escarpment and on the other side by the escarpment leading to the saline Lake Magadi. The ranch is dissected by the Ewaso Ngiro River and the riparian woodlands following the watercourses as they descend the escarpment.

The study area experiences more extreme weather conditions than most surrounding areas. It is one of the lowest points in the district with a consequent high mean maximum temperature of 34°c. Estimated annual rainfall is 429mm, the lowest in the entire district.

The human population density of the ranch is estimated at 3-6 persons per square kilometre. The main economic activity of the ranch is pastoral production of livestock. This activity is dominated by the Maasai tribe and is based on nomadism - living and grazing livestock in different parts of the ranch during different seasons of the year. With tsetse control now implemented by the community on the ranch, cattle and other livestock can be seen more frequently in the riparian woodlands.

A more sweeping land use change to be seen in the area is a recent trend to demarcate individual land ownership boundaries particularly in the forest and to practice sedentary cultivation of horticultural crops intended for the export market. Under contract to vegetable exporters, farmers in Nguruman are cultivating crops previously unknown to them and using large quantities of purchased inputs including pesticides. Among the crops being cultivated in the area are the eggplant, bitter gourd (*Momordica charantia* L.) and okra (*Abelmoschus (Hibiscus) esculentus* L. Moench.). Of these crops the eggplant was selected as the study species.

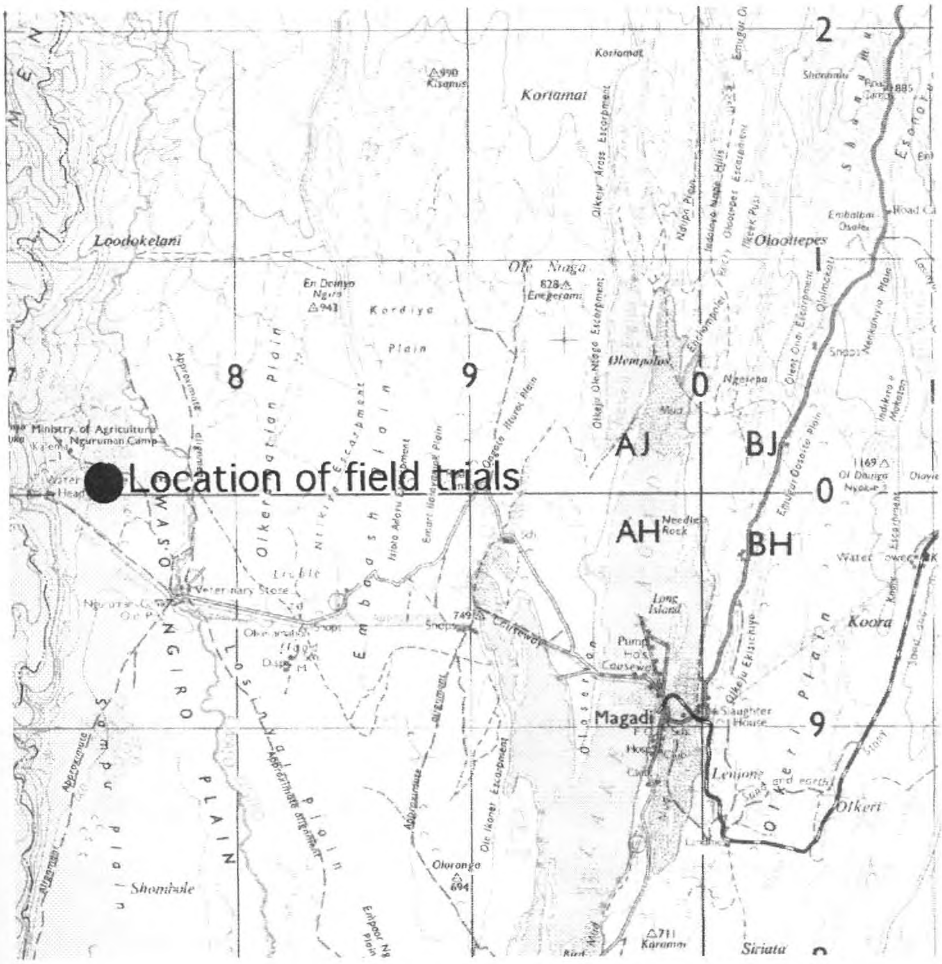

Figure 1. Map showing the location of the study site (Scale 1: 250,000).

CHAPTER 1

1.0 LITERATURE REVIEW.

1.1 Characteristics of the eggplant

The Leptostemonum group of the genus *Solanum*, to which the eggplant belongs, have spiny and stellate hairs, which can provide protection from grazing animals and from intensive sunlight in semi-desert and savanna habitats (D'Arcy, 1979).

A typical eggplant flower is pentamerous and hermaphrodite; solitary or in 2-5 flowered cymes. Leaves are opposite or sub-opposite, rounded, violet and ferruginous pubescent. The calyx is 2-5cm long, wooly and persistent, forming a distinct cup-shaped structure at its base. The corolla is curved, hairy beneath and glabrous within, light purple but deep purple at veins. The stamens are 1-1.2cm long alternating with the lobes of the corolla, free, erect and yellow with very short filaments that are flat at the base. Anthers are long and narrow forming a cone that surrounds the styles and opening into two terminal pores. The styles are relatively short or long with capitate lobed green stigma (Quagliotti, 1979). The flowering habit is peculiar; the flowers set right in the stem and first one appears, usually, on a definite internode that may vary from the fifth to the thirteenth according to the cultivar (Kakizaki, 1924). The peduncle sometimes bears 2 or 3 flowers but usually only one of them is fertile (Quagliotti, 1979).

1.2 Physiology of the Eggplant

Flower formation in the eggplant, which is classified as a day neutral plant, is considerably affected by nutritional factors. Fertilizer levels appear to cause more pronounced differences in time of flowering initiation and development than it does in those plants which respond to vernalisation and photoperiod (Eguchi *et al.*, 1958).

Flowering is staggered and lenghty for example, from the 100th to 120th day and the 250th day after sowing. In northern Italy flowering occurs from mid-June to the first ten days of November, with peaks halfway through July and at the beginning of September (Quagliotti, 1979). A characterisation of cultivation and flowering periods in an African region is not available in the literature.

The first opening of the flower occurs between 06:00 and 09:00 hours whilst dehiscence occurs between 05:00 and 08:00 hours. The flowers open in the morning but close again daily for between 8 to 10 days after the first day of opening (Pal & Singh, 1943). High humidity and temperature in the opening hours tend to hasten the opening of the flowers and the dehiscence of the anthers.

The corolla is visible in the calyx three to four days before it opens and the day before, it reaches or exceeds the calyx lobes. On opening, the exposed portion of the corolla bulges outward and clefts appear between petals; after complete opening they become reflexed.

1.3 Heterostyly in the eggplant

Heterostyly - the difference in the position of the stigma from the anther tips - depends on the occurrence of styles with different lengths, hypostigmatic (short), peristigmatic (medium), or epistigmatic (long) which in the eggplant are 3 - 4.5 mm, 6 - 7 mm and 7.5 - 9 mm respectively. The length of the stamens does not change in the three types of flowers whose frequency varies noticeably in different cultivars (Murtazov *et. al.*, 1971).

Uncini (1971) studied the influence of flower heterostyly on fruit setting in 34 eggplant cultivars. He found that secondary flowers of the inflorescence are hypostigmatic and lack fruit setting, which largely depends on the peristigmatic condition. peristigmatic flowers are more favourable to selfing than epistigmatic flowers, as they are less sensitive to the effect of visiting insects.

The high percentage of abortion in the short styled flowers is generally confirmed, whereas the efficiency of fruit setting of medium-styled flowers is not always accepted. The position of the flower in the inflorescence also appears to be important in controlling normal setting (Smith, 1931; Kirshnamuthi and Subramanian, 1954; Khot and Kaniktar, 1956; Oganesjan, 1966; Prasad and Prakash, 1968; Murtazov *et. al.*, 1971).

In most flowers the style projects from the cone of anthers, bending slightly downwards. In such long-styled flowers insects first make contact with the stigma. As the anthers dehisce by terminal pores, insects, wind or anything touching or shaking the anthers makes pollen fall. However, there is often so much dispersion of pollen that the stigma cannot receive a sufficient amount of it (Kakizaki, 1924).

1.4 Pollination of the Eggplant

1.4.1 Experiments in Bagging

Pal & Singh (1943) bagged entire plants in their studies on the pollination of the eggplant. They bagged 5 plants each of 'Muktakeshi' and 'Clustered White' cultivars with fine muslin bags at the commencement of flowering. After two and a half months the bags were removed and the number of fruits formed on the plants recorded. Two of five plants of 'Muktakeshi' had three fruits each, two had two fruits each and one had only one fruit. Open-pollinated plants of the same cultivar had an average of 20 fruits per plant formed during the same period. In 'Clustered White' cultivar the bagged plants had an average of two fruits per plant, in comparison with an average of fifteen fruits per plant on open pollinated plants.

In some plants twenty flowers were bagged in small muslin bags and only two fruits were set. On examination of the stigmas of the twenty bagged flowers, only five were found to have pollen grains on them. This shows that adequate pollination was not possible when flowers were bagged therefore the setting of fruits in the eggplant can therefore only occur as a result of cross-pollination (Pal & Singh, 1943).

In other plants bagged flowers were hand-pollinated and a setting of 80% was observed showing that the handling involved in the act of enclosing flowers with bags was not responsible for poor setting.

The experiments in bagging show that only a small proportion of the eggplants is self-pollinated. The question then arises as to what are the agencies responsible for pollination in nature.

1.4.2 Action of Gravity

Gravity can exert its full force in pollen escape from the anthers only if the flowers are hanging downwards. The fact that a majority of the flowers do not hang downwards but are borne more or less erect or at an angle with the vertical precludes the possibility of gravity being an important factor in pollination.

With the aid of copper wires, Pal & Singh (1943) kept twenty buds in a vertically downward position and a similar number in a vertically upward position. A wire mesh cage kept these buds covered until the petals had dried completely. A duplicate series

The action of gravity appeared to be insignificant as shown in section 1.4.2. The possibility of direct contact of the sexual organs is low since the stigmas usually protrude well beyond the anthers or are far below them and it is only rarely that the stigmas and anther tips are at the same level. There is no information regarding the extent to which insects small enough to enter the cages could be responsible for pollination but obviously this cannot be very much.

The difference in the number of seeds per unit fruit between the covered and uncovered plants is striking. 'Muktakeshi' cultivar averaged 210 seeds in covered plants and 987 seeds in uncovered plants while 'Clustered White' cultivar averaged 245 seeds in covered plants and 870 seeds in uncovered plants which suggests that lack of adequate pollination is responsible for poor setting of fruits and seeds.

1.4.4 Action of Insects

A large number of insects, primarily bees, have been recorded visiting the eggplant flowers in the morning hours, e.g., *Xylocopa, Apis, Anthophora* and *Polistes (*Pal & Singh, 1943). They touch the stigma with their bodies, carrying pollen grains from other flowers. Many trials indicate that these insects play a major role in pollination; consequently fertilisation is greatly improved by cross-pollination (Kakizaki, 1924; Magtang, 1936).

Stigmas visited by insects were examined under the microscope and it was found that the whole of the stigmatic surface was fully coated with pollen. The fruits resulting from such insect-pollinated flowers had a large number of seeds in each (Pal & Singh, 1943). Therefore, there is little doubt that insects play the major role in the pollination of eggplant flowers.

Abrol (1991) while studying the pollination of the eggplant in India observed seven species of bees belonging to four families were attracted to the eggplant flowers. Bumble bees, *Bombus asiaticus* Morawitz, 1875, *B. trifasciatus* Smith, 1852, and *B. simillimus* Smith, 1852 were the predominant visitors while honeybees, *Apis cerana, A. mellifera;* Carpenter bees, *Xylocopa valga* Gerstaecker, 1872 and *Lasioglossum* sp. visited less frequently and in small numbers. Bumble bees were efficient pollinators on the basis of their field behaviour, population dynamics, pollen carrying capacity and flower visitations in unit time.

Amoako & Yeboah-Gyan (1991) were able to show that the honeybee, *A. mellifera*, had a special role in the pollination of three solanaceous vegetable crops namely *Lycopersicon esculentum*, *Capsicum frutescens* and *Solanum melongena* in Ghana. Others have shown that honeybees and bumble bees are the main pollinators of the eggplant (Torregrossa, 1983; Tanda & Mann, 1985; Eijnde, 1994).

1.4.5 Buzz-pollination of the Eggplant

Solanum species bear flowers whose anthers dehisce by pores. The abundant pollen can only be removed through these small orifices, and bees have learnt to expel and efficiently harvest pollen from these flowers by vibrating their bodies while in contact with the stamen, effecting a process termed 'buzz-pollination'. This mode of pollination is called the buzz-pollination due to the audible buzz component of intra-floral bee behaviour during the rapid floral visitations.

The pollinators alight on the corollas and coil on the anther cones, grasping the stamens tightly with their mandibles while their wings are held in repose. They then contract their large indirect flight muscles and transmit vibrations throughout their bodies.

The body parts such as the thorax, abdomen and legs that are in direct contact with the anthers vibrate them very rapidly at a frequency of between 50 and 2000 Hz (Buchmann 1983) immediately causing the anthers, locules and sometimes the entire flower to vibrate with the same frequency as the thorax of the buzzing bee. This bee-induced floral vibration functions to loosen the locule-containing pollen, producing strong pollen grain-locule interaction that result in rapid expulsion of most of the pollen from the anther apices within a few seconds.

Since these flowers produce no floral nectar as a reward to the pollinator and have abundant pollen, it has been hypothesized that their pollen chemistry might be different from plants without anther pores and not requiring vibrational pollination (Buchmann 1983). The pollen of buzz pollinated flowers were determined to be more nutritious than those from other flowers, and specifically higher in protein content (Buchmann, 1983).

1.5 Measurement of Pollinator Effectiveness

Many of the organisms visiting a population of flowering plants are not pollinating agents but are pollen and nectar 'thieves' that do not benefit the plants. Before any meaningful investigations into pollen-pollinator systems can be undertaken it is imperative to determine the importance of a visiting species to the plant population under investigation. A measure of pollinator effectiveness is needed. The measure of pollinator effectiveness can be undertaken in two main ways, indirect and direct measures.

Indirect measures rely upon the pollen carried by the visitor as an indicator of effectiveness (Beattie, 1972; Ehrenfeld, 1979). These data are often further refined by determining the relative abundance of visitors, visitation rates to flowers and relative amounts of pollen transferred to stigmas (Primack & Silander, 1975).

Primack & Silander (1975) developed a quantitative approach for comparing the relative importance of alternative pollinators in terms of quantity, level of out-crossing and efficiency of pollen transferred. They used this method to investigate the pollination of *Oenothera fruticosa* L. by two pollinators, *Apis mellifera*, and the soldier beetles *Chauliognathus marginatus* Fab., 1875 (Coleoptera: Chauliognithidae).

The quantity of pollen transferred per unit time can be calculated as the mean number of grains transferred to the stigma of a flower visited per pollinator visit multiplied by the mean number of flowers visited per unit time. Likewise, the quantity of pollen transferred per unit time by a species of pollinators can be calculated as the number of foraging individuals of that species multiplied by the quantity of pollen transferred by that individual per unit time (Primack & Silander, 1975).

Pollen transferred within a plant produces no seeds in self-incompatible species and may result in low quality seeds in self-compatible species. The proportion of pollen transferred that are out-cross (between plants) pollen (P) can be calculated by considering the number of flowers visited per plant (N), the number of pollen grains transferred per visit (G) and the number of grains on the body of the pollinator (B). The equation for this calculation is given below:

$$P = (\frac{1}{N})\sum_{i=1}^{N}(1 - \tfrac{G}{B})^{N-i}$$

Indirect measurement of pollinator effectiveness has two advantages namely:

a) The parameters can quickly be determined, and

b) The data, though laborious to analyse are easy to collect.

The disadvantages of this method are:

a) The measures, even when refined, are difficult to relate directly to the contributions made by each visiting species to the plant's breeding success,

b) Amounts of pollen grains on the body of insects tell nothing of the number of pollen grains deposited on the stigma or the viability of the pollen on an insect's body and

c) Similarly, counting pollen grains indicate nothing about the quality of that pollen or the successful ripening of ovules in that flower (Spears, 1983).

Direct measurements of effectiveness are measures of seed set by a plant population in response to pollinator visits. Direct measures are commonly used in agricultural research (Alderz, 1966; Tepedino, 1981). Spears (1983) used this method in measuring the pollinator effectiveness of the pollinators of *Ipomea trichocarpa* Elliot (Convolvulacea).

There are three parameters used to determine pollinator effectiveness (PE) for a visiting species *(i)*, namely,

Z = mean number of seed set per flower by a plant population in the absence of pollinator visits,

U = mean number of seeds set per flower by a plant population with unrestrained visitation (this technique assumes that flowers with unrestrained visitation will average greater than a single visit during the life of the flower) and

P *(i)* = mean number of seeds set per flower by a plant population receiving a single visit from species *(i)*.

With these parameters, PE for each species can be calculated as:

$$PE = \frac{P_i - Z}{U - Z}$$

i.e., the proportion of unrestrained seed set caused by a single visit of species *(i)* corrected by the amount of seed set when no visitation occurs (Spears, 1983).

When artificially pollinating flowers in tests of pollinating effectiveness, the following points are important to obtain uniform levels of fruit setting and seed production:

- When preventing wind and insect pollination, choose the most suitable bags for isolation: embroidery cloth gives the best results (Bhore *et. al.*, 1965).
- The earliest single and long-styled flowers are least likely to abort. (Frydrych, 1964).
- A large quantity of pollen increases fruit set and the number of seeds per fruit and decreases the frequency of parthenocarpy (Popova, 1959).
- Stigma receptivity and fertilising capacity of pollen are highest at the same time of opening of the floral buds; however, satisfactory fertilisation can be obtained over a two-day interval (Tatebe, 1938; Mikaeljan, 1964).

1.6 The foraging strategies of pollinators

Pollinators encounter a vast array of potential food plants, which vary manifestly in their density, nutritional value, and ease of handling. Faced with this diversity a pollinator must decide where to search which species to feed from and in what sequence. Foraging should be concentrated in habitats where expectation of yields is greatest and upon those plants whose nectar or pollen, or both, is most efficiently harvested and provides necessary nutrients as well as calories.

Theory predicts that pollinators will differentiate between different plant species and form 'search images' of the most favorable species, because this behaviour permits efficient localisation of time and effort and maximises cost-benefit relationships. In fact, the tendency of individual pollinators to forage within a plant species for a period of time rather than forage at random among several suitable species is a typical form of behaviour (Free, 1993). The choice of a forage species is determined principally by the quality and quantity of the floral reward. The dominant factors affecting bee visits appear to be the abundance and sugar concentration of the nectar and chemical attractants in the pollen (Martin and McGregor, 1973).

Pollinators will evolve to become specialists if the density and quality of one or a few resource plants is high and if the resources are predictable in time and space (Levins and MacArthur, 1969). In general when the abundance of the preferred species in the diet increases, the number of less preferred species in their diet breadth decreases. Pollinators will broaden their diet and switch hosts more frequently as their environment becomes patchier in space and time and as patch size declines relative to foraging range (MacArthur 1972).

Movement patterns of pollinators have been studied extensively. In general, pollinators, just like predators, meander until a preferred flower is encountered and then increase their rate of turning, thereby remaining in the vicinity of the encountered flower (Chandler, 1969).

1.7 Justification and significance of the study

A direct consequence of sedentary cultivation in many regions of subsaharan Africa is the clearing of forests to create space for cultivation. The agricultural crops subsequently cultivated are generally not native to the area but the pollinators which service them are. Pollinators that persist as small areas of forest are cleared for cultivation, forage on wild plants as well as the cultivated crops. These wild plants, which are native to the area, serve as an alternative source of nutrition to the pollinators especially when the cultivated crops are not flowering.

By clearing the forests, the wild host plants are lost. This creates an imbalance in the pollination ecology of the area. Should forest clearing continue to intensify, the yields of the crops will decrease due to a reduction in pollination service by the pollinators. This pollination 'subsidy' which the natural environment provides to agriculture is important and one that is all too often only appreciated after it is lost.

Therefore, there is the need to develop an insight into the pollinator species of the agricultural or horticultural crops in areas currently undergoing early stages of agricultural development in order to establish the most prominent pollinator species among the many visiting insects. This enquiry should be developed further to enable farmers to know the measures they may take to stem environmental degradation that will impact their agricultural productivity.

CHAPTER 2

2.0 MATERIALS AND METHODS

2.1. Collection and identification of the pollinators of the eggplant

The principal pollinators of the eggplant, all of which were bees, were collected and voucher specimen sent to Connal Eardly in South Africa and Roy Snelling in the United States of America for identification. These specimens are currently stored in the Botany department at the University of Nairobi.

The collection procedure was based on that of Little (1972). The materials used in collection and preservation of the pollinators were sweepnets, killing jars, pinning blocks, insect pins, pinning boards and naphthalene balls.

The bees were killed in jars freshly charged with ethyl acetate. Dead bees were removed immediately to avoid discoloration. The walls of the jars were wiped periodically to avoid the formation of moisture.

The dead bees were pinned between the base of the front wings through the body. All insects and labels were pinned at a uniform height using a pinning block to assist in uniformity by pushing the insects gently to the correct height. The middle hole of the pining block was used to position the label bearing the collecting data and the lower hole used for additional labels that were needed.

2.2 Manipulation of eggplant pollination

Five treatments were performed on two eggplant cultivars (Early Long Purple and Black Beauty) to ascertain the degree to which insufficient pollination can limit the yields of the crop, namely,

1. Open pollination (unlimited visitation of flowers by thepollinators)
2. Autogamy (Spontaneous self -pollination)
3. Enhanced self-pollination (Hand pollination with pollen from the same flower)
4. Enhanced cross pollination (Hand-pollination with pollen from different flowers)
5. Wind pollination.

These manipulations were performed during the second growing season (May-July 1999). In all manipulations, the first flower to open from an inflorescence was used since studies have shown that they are larger and longer styled than the remainder (Free, 1993), and are least likely to abort (Frydrych, 1964). In addition, all manipulations were made on the second day of opening, when the stigmas were most receptive.

A split plot design was used. The main plot was divided into two sub-plots, one for each cultivar. The two sub-plots were further divided into five smaller blocks, each measuring 10 square meters. The five treatments were then randomly assigned to the blocks in each sub plot. The main assumptions here were that all the factors apart from those considered as treatments and the inherent differences between the two cultivars were uniform for all the experimental units.

In each treatment, the fruits were harvested after four weeks when they had matured. The fruits were dissected and their seeds were removed, dried and counted.

2.2.1. Evaluation of the effect of open pollination

The flowers were tagged and left unbagged to allow free visitation by the pollinators.

2.2.2. Evaluation of the effect of enhanced cross-pollination

Flowers were emasculated before anther dehiscence, bagged (using brown paper bags to prevent both wind-borne pollen and insect pollinators), and upon opening, pollen from different flowers of different plants were artificially transferred to their stigmas using a pair of sharp pointed forceps. The flowers were then bagged again.

2.2.3. Evaluation of autogamy

Flowers were bagged as above and left untreated so that the pollen source was from the same flower.

2.2.4. Evaluation of enhanced self-pollination

Flowers were bagged as above and on opening, pollen from the same flowers was artificially transferred to their stigmas.

2.2.5. Testing the action of wind.

A plant cage was placed over each of the 2 blocks where the action of wind as an agent of pollination was to be tested. 50 flowers of plants from each cultivar were randomly chosen, emasculated to prevent self-pollination and tagged. The plant cage served to exclude insects but permitted wind-borne pollen to reach the stigmas.

2.3 Studying the visitation patterns of eggplant pollinators

The study was done during the months of November-December 1998, and in May-June 1999. The effect that three factors namely, (1) time of the day, (2) prevailing ambient temperature and (3) the resource abundance (number of flowers per square meter) had on the total number of foraging pollinators and the total number of flowers that the pollinators visited was investigated.

The observations were made in standardized plots, each measuring one square meter, that were distributed randomly in the eggplant fields. The observations were made over 10-minute period intervals starting from 06:30 a.m. to 12:30 noon, for after 12.00 noon there was a reduction in the number of pollinators that were seen in the fields, suggesting that this was past the optimal time of foraging by the pollinators.

2.3.1 Effect of time.

The 10-minute observation periods were grouped together in one-hour intervals beginning from 06:30 a.m. to 12:30 p.m. The effect of time on the visitation patterns of the pollinators in the two eggplant cultivars was studied together since the crops were grown adjacent to one another and the pollinators foraged the adjacent fields moving between the cultivars without breaking their foraging trips in between. An ANOVA (Procedure GLM, SAS) was then performed to test if there was a significant difference in the number of foraging pollinators within the hourly time intervals.

2.3.2. Effects of temperature and resource abundance

The effects of temperature and the resource abundance on the number of foraging pollinators and the number of flowers visited by the foraging pollinators was also studied. The number of open flowers in each standardized plot was counted at the beginning of each 10-minute interval. At the end of every 10-minute interval, the ambient temperature readings were taken using a thermometer that was placed one meter above the ground under a shade.

Two multiple linear regression analyses (Procedure Reg, SAS) were performed to test if,

1. The number of foraging pollinators increased linearly as temperature and the number of open flowers in each standardized plot increased
2. The number of flowers visited by the foraging pollinators increased linearly as temperature and the number of open flowers in each standardized plot increased

2.4 Evaluation of the pollination efficiency of each pollinator species

Pollinator efficiency was measured using Spears' (1983) method, which measures seed set by a plant population in response to pollinator visits. Three parameters were used to determine pollinator effectiveness (PE) for a visiting species *(i)*, namely,

Z = mean number of seed set per flower by a plant population in the absence of pollinator visits

U = mean number of seeds set per flower by a plant population with unrestrained visitation.

P *(i)* = mean number of seeds set per flower by a plant population receiving a single visit from species *(i)*.

With these parameters, PE for each pollinator species can be calculated as:

$$PE = \frac{P_i - Z}{U - Z} \qquad \ldots \textit{equation 1.}$$

i.e. the proportion of unrestrained seed set caused by a single visit of species *(i)* corrected by the amount of seed set when no visitation occurs.

This technique assumes that flowers with unrestrained visitation will average greater than a single visit during the life of the flower.

Young flower buds were bagged a day before they opened to exclude pollinators. On the second day after the flower had opened, the bags were removed and the flowers were allowed only a single visit by a pollinator. The flower was then bagged again until the fruits had matured. The fruits were then dissected and the number of seeds that were set in each fruit were counted, noting which treatment had been performed to its parent flower.

2.5 Determination of alternative resources

The pollinators were monitored in the surrounding wild habitat and the plant species used for forage were noted based on the method of survey of Silveira and Godinez (1996). A 5km long and 2m wide transect traversing through the farms and the surrounding wild habitat was established. This transect was surveyed at a constant pace, and only the eggplant pollinators seen foraging on flowers of plants along it were collected. The numbers of each pollinator species that were found foraging on a particular plant species was also noted if they could not be collected.

During the exercise, care was taken to avoid staying at one point waiting for more pollinators to arrive. This ensured that the alternative forage plants were surveyed in proportion to their relative abundance and that the pollinators were also collected in numbers proportional to their relative frequencies in the area. The plant species visited by pollinators were collected and taken for identification at the University of Nairobi herbarium.

Since the activity of pollinators varies through the day and different species may concentrate their activity at different times of the day, the transect was surveyed at different times of the day. To standardize the collections and make data comparable, the total time spent per habitat was noted. This assisted in comparison of the relative abundance of bees (number of recorded specimen divided by the total number of hours).

2.2.1. Evaluation of the effect of open pollination

The flowers were tagged and left unbagged to allow free visitation by the pollinators.

2.2.2. Evaluation of the effect of enhanced cross-pollination

Flowers were emasculated before anther dehiscence, bagged (using brown paper bags to prevent both wind-borne pollen and insect pollinators), and upon opening, pollen from different flowers of different plants were artificially transferred to their stigmas using a pair of sharp pointed forceps. The flowers were then bagged again.

2.2.3. Evaluation of autogamy

Flowers were bagged as above and left untreated so that the pollen source was from the same flower.

2.2.4. Evaluation of enhanced self-pollination

Flowers were bagged as above and on opening, pollen from the same flowers was artificially transferred to their stigmas.

2.2.5. Testing the action of wind.

A plant cage was placed over each of the 2 blocks where the action of wind as an agent of pollination was to be tested. 50 flowers of plants from each cultivar were randomly chosen, emasculated to prevent self-pollination and tagged. The plant cage served to exclude insects but permitted wind-borne pollen to reach the stigmas.

2.3 Studying the visitation patterns of eggplant pollinators

The study was done during the months of November-December 1998, and in May-June 1999. The effect that three factors namely, (1) time of the day, (2) prevailing ambient temperature and (3) the resource abundance (number of flowers per square meter) had on the total number of foraging pollinators and the total number of flowers that the pollinators visited was investigated.

The observations were made in standardized plots, each measuring one square meter, that were distributed randomly in the eggplant fields. The observations were made over 10-minute period intervals starting from 06:30 a m. to 12:30 noon, for after 12.00 noon there was a reduction in the number of pollinators that were seen in the fields, suggesting that this was past the optimal time of foraging by the pollinators.

2.3.1 Effect of time.

The 10-minute observation periods were grouped together in one-hour intervals beginning from 06:30 a.m. to 12:30 p.m. The effect of time on the visitation patterns of the pollinators in the two eggplant cultivars was studied together since the crops were grown adjacent to one another and the pollinators foraged the adjacent fields moving between the cultivars without breaking their foraging trips in between. An ANOVA (Procedure GLM, SAS) was then performed to test if there was a significant difference in the number of foraging pollinators within the hourly time intervals.

2.3.2. Effects of temperature and resource abundance

The effects of temperature and the resource abundance on the number of foraging pollinators and the number of flowers visited by the foraging pollinators was also studied. The number of open flowers in each standardized plot was counted at the beginning of each 10-minute interval. At the end of every 10-minute interval, the ambient temperature readings were taken using a thermometer that was placed one meter above the ground under a shade.

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Since the activity of pollinators varies through the day and different species may concentrate their activity at different times of the day, the transect was surveyed at different times of the day. To standardize the collections and make data comparable, the total time spent per habitat was noted. This assisted in comparison of the relative abundance of bees (number of recorded specimen divided by the total number of hours).

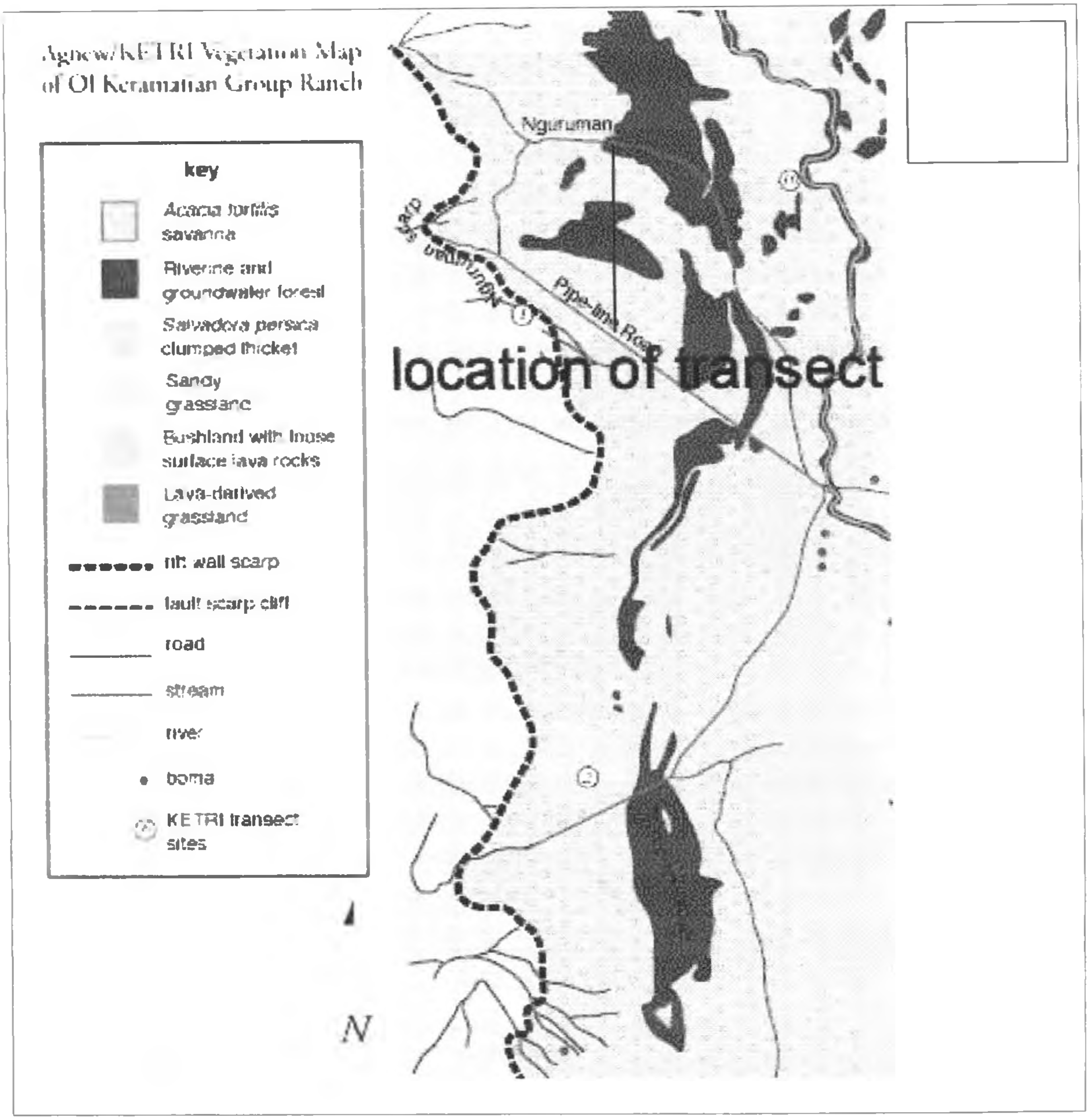

Figure 2. Map showing the location of transect (Agnew *et. al.*, 2000). Scale 1:200000.

CHAPTER 3

3.0 RESULTS

3.1 The eggplant pollinators

The pollinators were all bees belonging to 2 families, Apidae and Halictidae. A total of 10 bee species were collected from the eggplant fields. All the 10 were observed visiting the eggplant blossoms. The table below categorises the pollinators according to their families.

FAMILY	SPECIES
Apidae	*Amegilla calens* Lepeletier, 1841
Apidae	*Amegilla nubica*
Apidae	*Apis mellifera* Linn.
Apidae	*Crosisaspidia* sp. Ashmead
Apidae	*Xylocopa albiceps* Fabricius, 1804
Apidae	*Xylocopa caffra* Vachal, 1897
Apidae	*Xylocopa flavobicincta* Gribodo, 1884
Apidae	*Xylocopa flavorufa* Smith, 1874
Halictidae	*Nomia* sp. Latrielle, 1804
Halictidae	*Pseudapis* sp. Kirby

Table 1. The families of the eggplant pollinators

A. nubica, Crocisaspidia sp. and *X. flavobicincta* were made in casual collections in the eggplant fields and did not feature much in the visitation studies. All the collected pollinators, except the honeybee (*Apis mellifera*) were capable of effecting buzz-pollination.

Plate 1. *Xylocopa caffra* Vachal, 1874

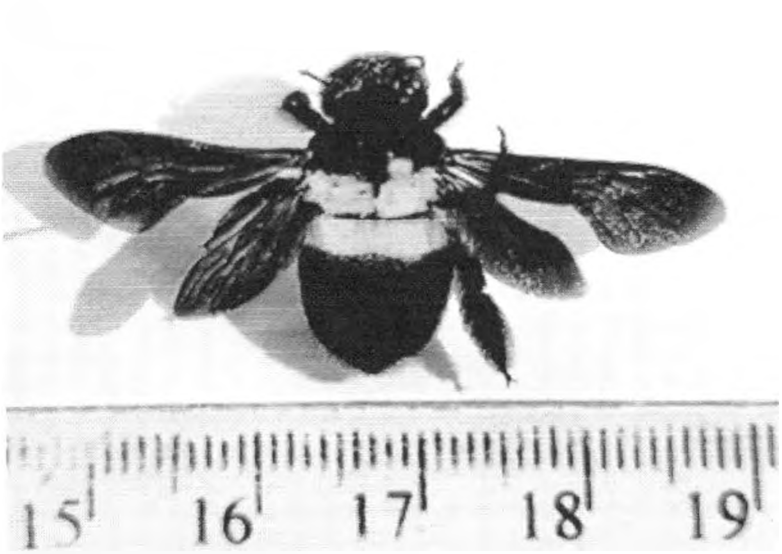

Plate 2. ***Amegilla calens*** **Lepeletier, 1841**

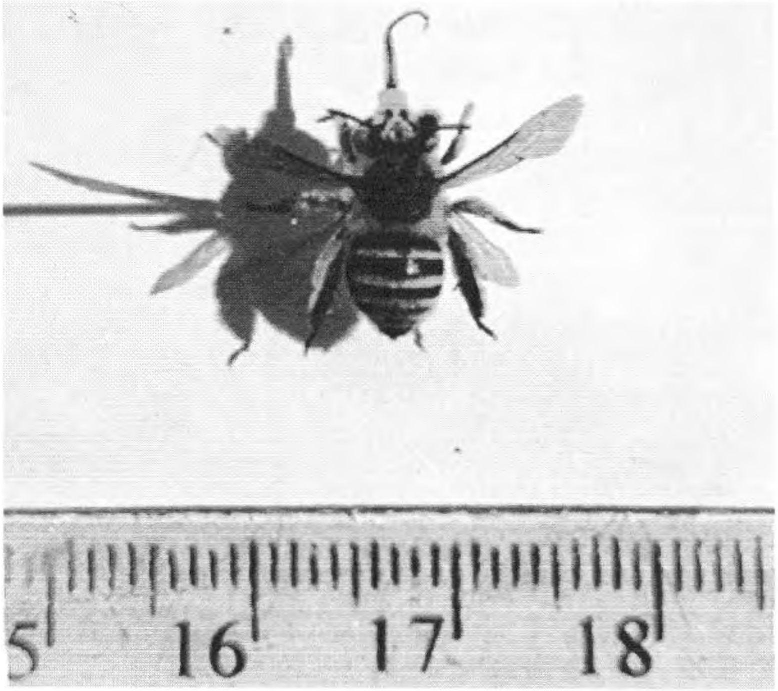

Plate 3. ***Amegilla nubica***

Plate 4. *Crosisaspidia* sp. Ashmead

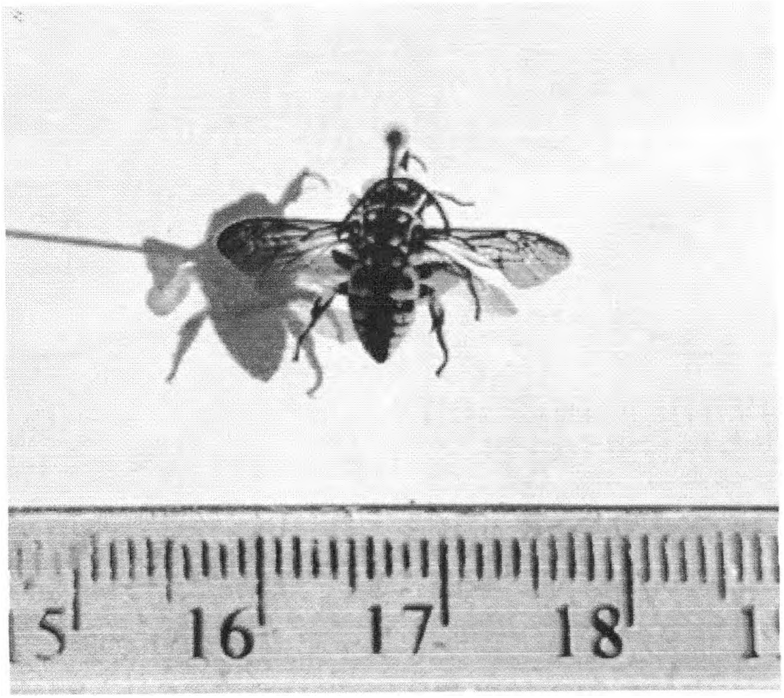

Plate 5. *Xylocopa albiceps* Fabricius, 1804

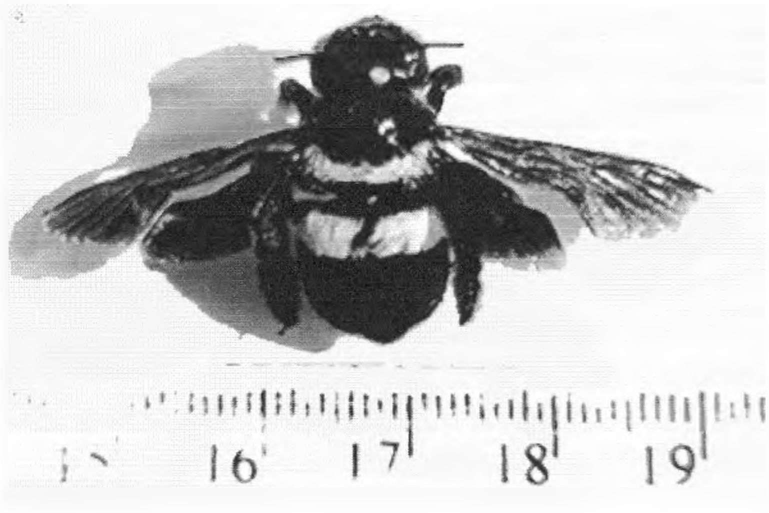

Plate 6. *Xylocopa flavorufa* Smith 1874

Plate 7. *Xylocopa flavobicincta* Gribodo, 1884

Plate 8. *Nomia* sp. Latreille 1804

Plate 9. *Pseudapis* sp. Kirby

Plate 10. ***Apis mellifera*** **Linn.**

3.2 Manipulations of eggplant pollination the extent to which insufficient pollination can limit the crop's yield

An ANOVA was performed to compare the effects of each treatment on the number of seeds per fruit.

3.2.1. Insufficient pollination tests in the Early Long Purple.

An ANOVA (Statview 4.5, Macintosh version) was performed to determine if there was a significant difference in seed set resulting from the different treatments (four levels). There were no fruits that were formed in caged plants that were used to test the contribution of wind pollination. All the fifty flowers aborted and this treatment was not included in the model.

Model: $\mathbf{Y}_{ijk} = \mu + \mathbf{t}_{i=1..4} + \mathbf{e}_k$

Where $\mathbf{Y}$ = seed set, μ = mean of observations, $\mathbf{t}$ = treatment and $\mathbf{e}$ = error.

Source	DF	Sum of Squares	Mean Square	F-Value	P-Value
Treatment	3	26018074.560	8672691.520	18.918	<0.0001
Residual	169	77475606.122	458435.539		

Table 2. ANOVA table for seed set.

Effect: treatment

Treatment	N	Mean	Std. Dev.	Std. Err.
Open pollination	43	571.860	578.297	88.190
Autogamy	53	229.302	460.978	63.320
Enhanced selfing	29	928.241	764.191	141.907
Enhanced crossing	48	1201.229	875.529	126.372

Table 3. Means Table for seed set

Seed set was greatest in fruits that resulted from enhanced cross-pollination. Enhanced self-pollination also resulted in high seed set. The third highest seed set resulted from the open pollinated flowers. Autogamy resulted in the lowest seed set and most of these flowers aborted before maturity. Figure 3 shows the interaction bar plot of seed set due to the four different treatments. A Bonferroni/Dunn means comparison test was also done to compare the mean seed set between the different modes of pollination.

Effect: treatment
Significance Level: 5 %

Comparisons	**Mean Diff.**	**Crit. Diff**	**P-Value**
Open pollination, autogamy	342.559	370.988	0.0147 *
Open pollination, Enhanced selfing	-356.381	434.340	0.0299 *
Open pollination, Enhanced crossing	-629.369	379.544	<0.0001**
Autogamy, Enhanced selfing	-698.939	417.510	<0.0001**
Autogamy , Enhanced crossing	971.927	360.163	<0.0001**
Enhanced selfing, Enhanced crossing	-272.988	425.131	0.0883

Table 4. Bonferroni/Dunn test for seed set. * shows observations that were significant at 5% significance level while **are significant at 1% significance level.

All treatments except the enhanced self-pollination and enhanced cross-pollination experiments treatments differed significantly at 1% level.

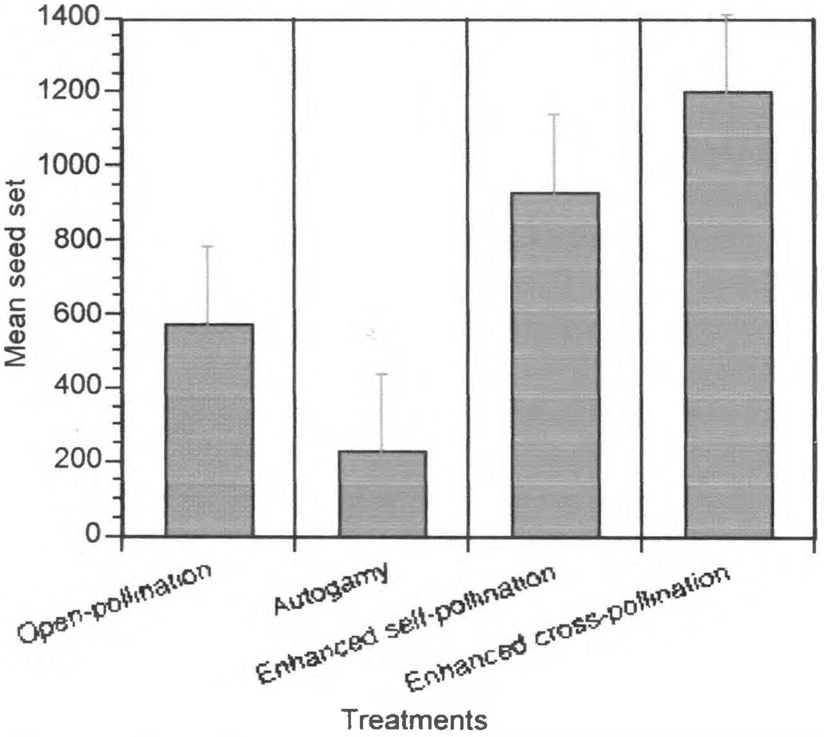

Figure 3. Interaction bar plot for seed set in the Early Long Purple due to four different treatments ($p < 0.0001$, $n = 200$).

3.2.2. Insufficient pollination tests in the Black Beauty

An ANOVA (Statview 4.5, Macintosh version) was performed to determine if there was a significant difference in seed set resulting from the different treatments (four levels). Only one fruit was set in the 50 wind pollinated flowers that were covered by a plant cage and the treatment has not been included in the model. This fruit weighed 186 g and had 992 seeds.

Model: $\mathbf{Y}_{ijk} = \mu + \mathbf{t}_{i=1..4} + \mathbf{e}_k$

Where $\mathbf{Y}$ = seed set, μ = mean of observations, $\mathbf{t}$ = treatment and $\mathbf{e}$ = error.

The overall model was significant (table 5, $p = 0.0002$). Enhanced cross-pollination resulted in the highest mean seed set, followed by open-pollination and enhanced self-pollination respectively. Autogamy resulted in the lowest seed set. Figure 4 shows the interaction bar plot of seed set due to the four different treatments.

Source	DF	Sum of Squares	Mean Square	F-Value	P
Treatment	3	52774386.012	17591462.004	6.962	0.0002
Residual	196	495258258.768	2526827.851		

Table 5. ANOVA Table for seed set

Effect: Treatment

Treatment	N	Mean	Std. Dev.	Std. Err.
Open-pollination	48	2140.854	1944.689	280.692
Autogamy	50	952.400	1283.122	181.461
Enhanced selfing	52	1935.846	1493.058	207.050
Enhanced crossing	50	2255.860	1585.322	224.198

Table 6. Means Table for seed set

A Bonferroni/Dunn means comparison test was also done to compare the mean seed set between the different modes of pollination.Seed set in fruits arising from three treatments namely, open pollination, enhanced self-pollination, and enhanced cross-pollination did not differ significantly (Table 7). However, the seed set in these categories differed significantly from seed set in self-pollinated flowers.

Effect: treatment
Significance Level: 5 %

Comparison	Mean Diff.	Crit. Diff	P-Value
Open-pollination, Autogamy	1188.454	856.134	0.0003 S
Open-pollination, Enhanced selfing	205.008	848.031	0.5201
Open-pollination, Enhanced crossing	-115.006	856.134	0.7207
Autogamy, Enhanced selfing	-983.446	839.166	0.0021 S
Autogamy, Enhanced crossing	-1303.460	847.353	<.0001 S
Enhanced selfing, Enhanced crossing	-320.014	839.166	0.3107

Table 7. Bonferroni/Dunn for seed set in the Black Beauty cultivar

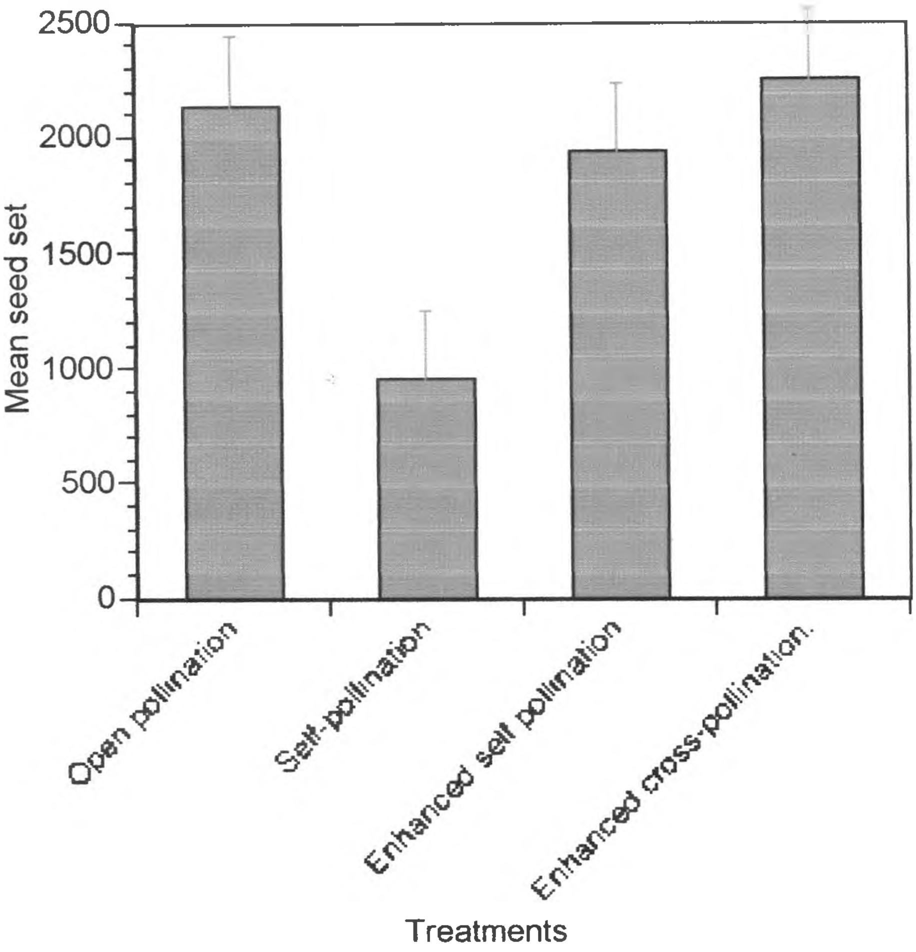

Figure 4. Interaction bar plot for seed set between four different treatments in the Black Beauty (p = 0.002, n = 200). Means, N values at data points and the standard error of means are given in table 6.

3.3 Visitation patterns of the eggplant pollinators.

3.3.1 Effect of time

3.3.1.1 Effect of time on the number of foraging pollinators

An ANOVA (Procedure GLM, SAS) was performed to test if there was any difference in the number of foraging pollinators that were observed in the hourly time interval. Two factors were included in the model namely time interval and the species to which the pollinator(s) belonged. Time interval had 6 level (06.30 -7.29 a.m., 7.30 - 8.29 a.m., 8.30

- 9.29 a.m., 9.30 - 10.29 a.m., 10.30 - 11.29 a.m. and 11.30 - 12.30 p.m.) where as there were5 levels of pollinator species (*X. caffra*, *Nomia* sp., *A. mellifera*, *A. calens* and others). Others consisted of *X.albiceps*, *X. flavorufa*, and *Pseudapis* sp., which, occurred at low frequencies.

Model: $\mathbf{Y}_{ijk} = \mu + \mathbf{t}_{i=1..6} + \mathbf{p}_{j=1..4} + \mathbf{e}_k$

Where $\mathbf{Y}$ = number of foraging pollinators, μ = mean of observations, $\mathbf{t}$ = time interval $\mathbf{p}$ = species to which the observed pollinator belonged to and $\mathbf{e}$ = error.

Dependent Variable: Number of foraging pollinators

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	24	178.14868563	7.42286190	2.31	0.0009
Error	193	619.96599327	3.21225903		
Total	217	798.11467890			

Source	DF	Type I SS	Mean Square	F Value	Pr > F
Time interval	5	12.72156546	2.54431309	0.79	0.5566
Pollinators species	4	104.48871771	26.12217943	8.13	0.0001
INTERVAL*POLL	20	60.93840246	4.06256016	1.26	0.2279

Table 8. ANOVA table for number of foraging pollinators.

The overall ANOVA model was significant (p = 0.0009). The effect of the time interval was not significant (p = 0.5566) showing that time did not play any role in determining the number of bees that were found foraging in the eggplant fields. The interaction between time interval and pollinator species was not significant either (p = 0.2279). The effect of the pollinator species was significant, implying that there was a significant difference in the number of bees belonging to different species that foraged at the different time intervals (Figure 5).

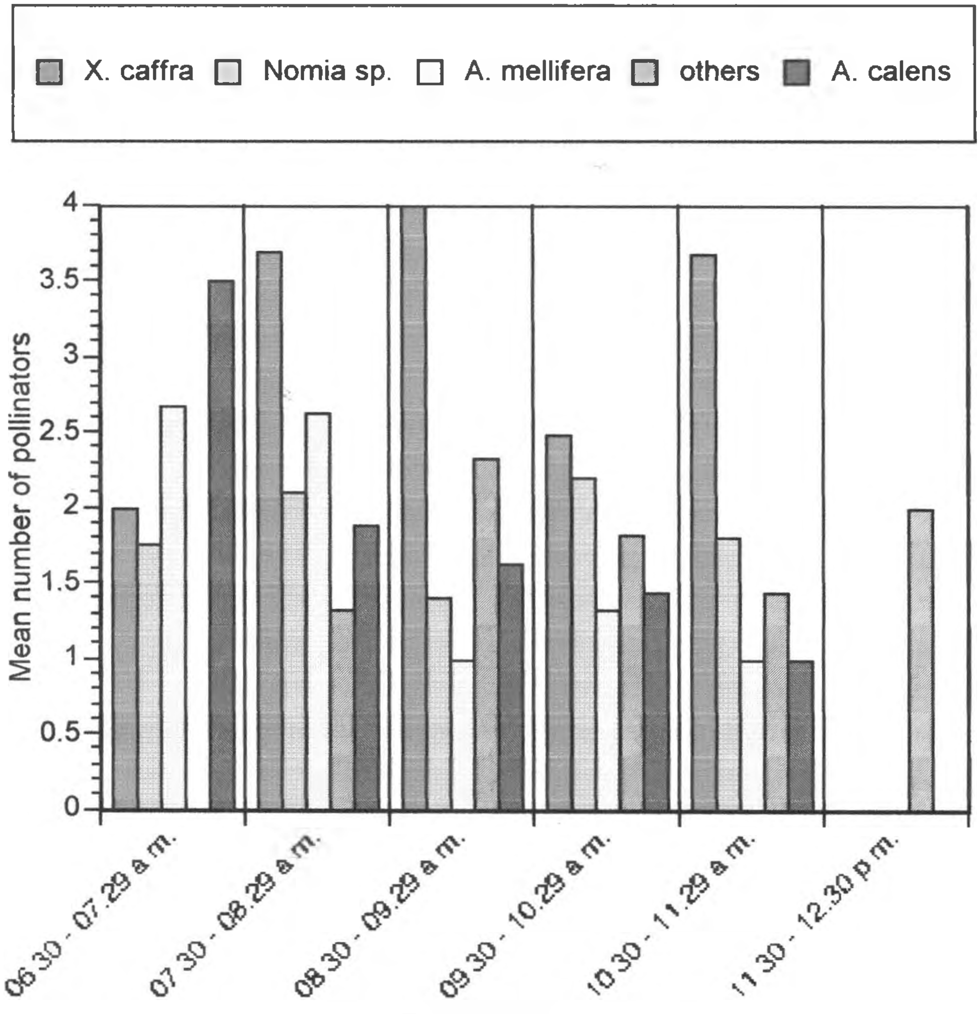

Figure 5. Interaction bar showing the change in number of pollinators with time (p 0.0009, n = 218).

3.3.1.2. Effect of time on the total number of flowers visited

An ANOVA (Procedure GLM, SAS) was performed to test if there was any difference in the total number of flowers visited by each pollinator within the time intervals. The factors included in the model remained the same as in section 3.3.1.1.

Model: $\mathbf{Y}_{ijk} = \mu + \mathbf{t}_{i=1..6} + \mathbf{p}_{j=1..4} + \mathbf{e}_k$

Where $\mathbf{Y}$ = number of flowers visited by each pollinator, μ = mean of observations, $\mathbf{t}$ = time interval $\mathbf{p}$ = species to which the observed pollinator belonged to and $\mathbf{e}$ = error.

Dependent Variable: VISITS

Source	**DF**	**Sum of Squares**	**Mean Square**	**F Value**	**Pr > F**
Model	24	4611.0611788	192.1275491	2.61	0.0002
Error	193	14214.5580873	73.6505600		
Total	217	18825.6192661			

Source	**DF**	**Type I SS**	**Mean Square**	**F Value**	**Pr > F**
Time interval	5	535.2376600	107.0475320	1.45	0.2070
Pollinator species	4	3208.636451	802.1591128	10.89	0.0001
INTERVAL*POLL	15	867.1870677	57.8124712	0.78	0.6934

Table 9. ANOVA table for number of floral visits

Again, the model was significant (p = 0.0002). The time interval did not significantly affect the number of flowers that the bees visited (p = 0.2070). However, there was a significant difference in the number of flowers visited by the different bee species (p = 0.0001) as shown in figure 6. The interaction effect between the time intervals and the pollinator species was not significant though (p = 0.6934).

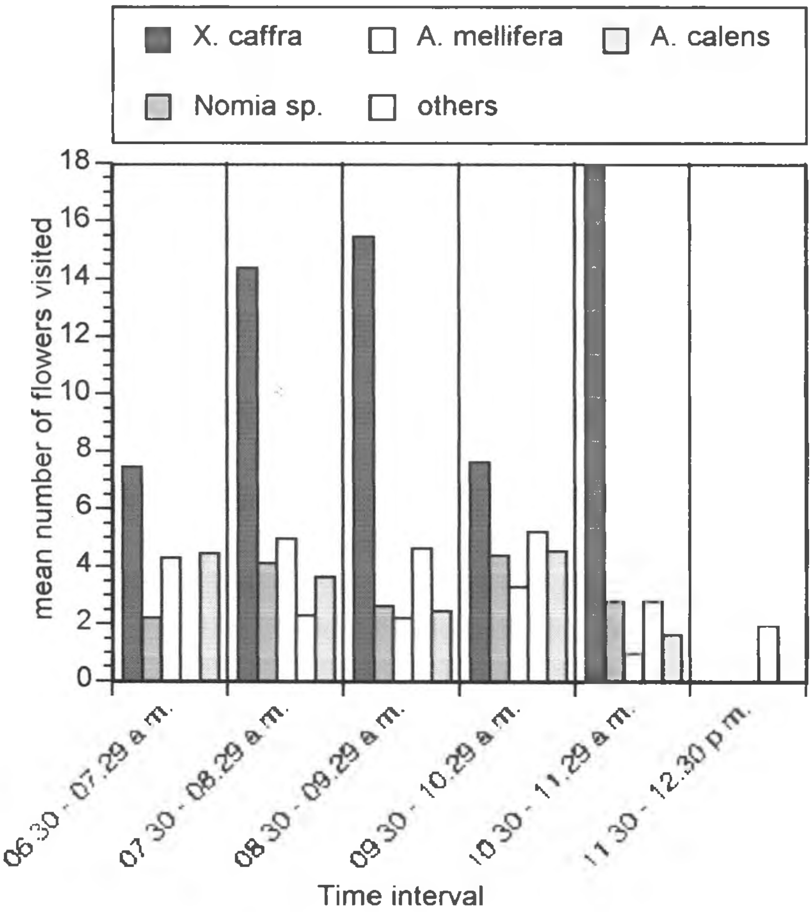

Figure 6. Interaction bar plot showing the change in the number of flowers visited by each bee species over time (p = 0.0002, n = 218).

A Duncan's multiple range tests was performed to compare the difference in mean visits as affected by the pollinator species and time intervals. The number of flowers visited by *X. caffra* were significantly higher than those visited by the other pollinator species. On the other hand, the total number of flowers visited by the bees did not differ over time.

Duncan Grouping	Mean	N	Pollinator species
A	11.640	75	*X caffra*
B	3.733	30	Others
B	3.583	24	*A. mellifera*
B	3.509	53	*Nomia* sp
B	3.222	36	*A. calens*

Table 10. Duncan's multiple range test for visits as affected by the pollinator species. Means with the same letters are not significantly different.

Duncan Grouping	Mean	N	Time interval
A	8.343	67	09.30 - 10.29 a.m.
A	7.778	9	11.30 - 12.30 p.m.
A	6.457	35	08.30 - 09.29 a.m.
A	5.045	66	10.30 - 11.29 a.m.
A	4.528	36	07.30 - 08.29 a.m.
A	4.400	5	06.30 - 07.29 a.m.

Table 11. Duncan's multiple range test for visits as affected by the pollinator species. Means with the same letters are not significantly different.

3.3.2. Effects of temperature and resource abundance

Two multiple linear regression analyses (Procedure Reg, SAS) were performed to test if temperature and flower density had a linear relationship with the number of observed pollinators and the number of flowers visited by the pollinators. A backward elimination procedure was used. This procedure includes all factors in the model and eliminates them one by one until the model becomes significant.

Models:

1. $y_1 = \beta_O + \beta_1 X_1 + \beta_2 X_2 + \text{error}$

2. $y_2 = \beta_O + \beta_1 X_1 \square + \beta_2 X_2 + \text{error}$

Where,

y_1 = (log10 (number of pollinators + 1). The counted number of pollinators was log transformed since the attraction of insects to any stimulus is not normal.

y_2 = number of flowers visited by the pollinators

β_O = intercept, β_1 & β_2 = slopes of line of best fit, X_1 = time, X_2 = number of flowers per square meter.

3.3.2.1 Effects of temperature and resource abundance on the number of pollinators that foraged the fields

	DF	sum of squares	Mean Square	F	Prob > F
Regression	2	1.95943832	0.97971916	1.84	0.1629
Error	118	62.73947846	0.53169050		
Total	120	64.69891677			

Parameter estimates

Variable	Estimate	Std. Err.	Type II SS	F	Prob > F
Intercept	0.12117516	0.61303084	0.02077406	0.04	0.8436
Temp.	0.04319890	0.02252511	1.95555729	0.68	0.0576
Flower	-0.00082770	0.00361941	0.02780519	0.05	0.8195

Table 12. Step 0. Backward elimination procedure for dependant variable Log10 (number of pollinators +1)

The model was insignificant (p = 0.1629) when all the factors were included and thus the most non-significant factor - number of flowers per square meter - was removed from the model and the regression analysis was run again.

	DF	Sum of Squares	Mean Square	F	Prob>F
Regression	1	1.93163312	1.93163312	3.66	0.0581
Error	119	62.76728365	0.52745617		
Total	120	64.69891677			

Parameter estimates

Variable	Estimate	Std. Err.	Sum of Squares	F	Prob>F
Intercept	0.10267225	0.60524334	0.01517863	0.03	0.8656
Temp	0.04281351	0.02237235	1.93163312	3.66	0.0581

Table 13. Step 1. Backward elimination procedure for dependant variable Log10 (number of pollinators +1)

With temperature as the only factor he model was still slightly insignificant (p = 0.0581). Temperature remained the only significant factor that affected the number of foraging pollinators that were observed foraging in the fields at 10% significance level. There was a linear increase in the number of pollinators that forged in the fields as temperature rose. The number of foraging pollinators did not increase linearly with the floral density increased.

3.3.2. Effects of temperature and resource abundance on the number of flowers visited by the pollinators

All Variables Entered R-square = 0.05874891 C(p) = 3.00000000

	DF	Sum of Squares	Mean Square	F	Prob>F
Regression	2	8.97787529	4.48893765	3.68	0.2081
Error	118	143.83985700	1.21898184		
Total	120	152.81773229			

Parameter estimates

Variable	Estimate	Std. Err	Sum of Squares	F	Prob>F
Intercept	-0.54736907	0.92822122	0.42389155	0.35	0.5565
Temp	0.09145479	0.03410641	8.76472115	7.19	0.0084
Flowers	-0.00338472	0.00548033	0.46497558	0.38	0.5380

Table 14. Step 0 for backward elimination procedure for dependant variable number of flowers visited by the pollinators

The model was not significant with all the factors were included. The number of flowers per square meter was the most non-significant and it was therefore removed from the model and the regression analysis was run again.

Variable Flower/m^2 removed R-square = 0.05570623 C(p) = 1.38144587

	DF	Sum of Squares	Mean Square	F	Prob>F
Regression	1	8.51289971	8.51289971	7.02	0.0092
Error	119	144.30483258	1.21264565		
Total	120	152.81773229			

Parameter estimate

Variable	Estimate	Std. Err	Sum of Squares	F	Prob>F
Intercept	-0.62303357	0.91770646	0.55891946	0.46	0.4985
Temp	0.08987880	0.03392231	8.51289971	7.02	0.0092

Table 15. Step 1 for backward elimination procedure for dependant variable number of flowers per square meter

The model became significant upon withdrawal of flowers/sq. meter (p = 0.0092). Temperature was the only significant factor that affected the number of flowers visited by the pollinators. There was a linear increase in the number of flowers visited by the pollinators as temperature rose.

3.4. Testing the pollination efficiency of the eggplant pollinators

3.4.1. Testing pollinator efficiency (PE) in the Early Long Purple

During the first growing season (November-December, 1998), only the Early Long Purple was studied. Five pollinator species occurred frequently enough to be considered in the study. These five species were, *X. caffra*, *A. calens*, *Nomia* sp., *A. mellifera*, and *Pseudapis sp.*

The pollinator efficiency (PE) for each species was calculated using the formula:

$PE = \frac{P_i - Z}{U - Z}$ Where,

Z = mean number of seed set per flower by a plant population in the absence of pollinator visits in this case 229.302 (obtained from the insufficient pollination tests).

U = mean number of seeds set per flower by a plant population with unrestrained visitation, in this case 571.860 (also obtained from insufficient pollination tests).

P*(i)* = mean number of seeds set per flower by a plant population receiving a single visit from species *(i)*.

The P_i for the five-pollinator species was;

X. caffra = 303.071 *A. calens* = 348.167 *Nomia* sp. = 685.400,

A. *mellifera* = 253.333 *Pseudapis* sp. = 381.643.

Pollinator species	**P_i**	**U**	**Z**	**P_i - Z**	**U - Z**	**PE**
X. caffra	303.071	571.860	229.302	74.558	342.558	0.218
A. calens	348.167	571.860	229.302	118.865	342.558	0.345
Nomia sp.	685.400	571.860	229.302	456.098	342.558	1.331
A. mellifera	253.333	571.860	229.302	24.028	342.558	0.007
Pseudapis sp.	381.643	571.860	229.302	152.341	342.558	0.445

Table 16. Pollinator efficiency in the ELP during the 1st growing season

Nomia sp. had the highest pollinator efficiency at 1.331. The pollinator efficiencies of, *Pseudapis* sp., *A. calens*, *X. caffra*, and *A. mellifera* were 0.445, 0.347, 0.217, and 0.07 respectively in a descending order.

Only two out of the 10 pollinator species were frequent enough to be considered in the test for pollinator efficacy during the second growing season (May-July, 1999). These two species were *X. caffra* and *Nomia* sp. The pollinator efficiency was calculated as before with Z as 229.302 and U as 571.860.

P (i) for the bees were,

X. caffra = 1410.368 *Nomia* sp. = 1125.143

Pollinator species	**P_i**	**U**	**Z**	**P_i - Z**	**U - Z**	**PE**
X. caffra	1410.368	571.860	229.302	1181.066	342.558	3.447
Nomia sp.	1125.143	571.860	229.302	895.841	342.558	2.615

Table 17. Pollinator efficiency in the ELP during the 2nd growing season

The results indicate that during the second season the crop productivity was much higher in general and *X. caffra* was much more efficient.

3.4.2 Testing pollinator efficiency in the Black Beauty

In the Black Beauty the PE was only tested during the second season (May-July 1999). The bees tested were *X. caffra* and *Nomia* sp. The pollinator effectiveness (PE) was calculated as before with Z as 952.40 and U as 2140.854

P (i) for the bees were, *X. caffra* = 3563.053 *Nomia* sp. was 2592.585

Pollinator species	**P_i**	**U**	**Z**	**P_i - Z**	**U - Z**	**PE**
X. caffra	3563.053	2140.854	952.40	2610.653	1188.45	2.197
Nomia sp.	2592.585	2140.854	952.40	1640.185	1188.45	1.38

Table 18. Pollinator efficiency in the Black beauty Cultivar

In general, the PE of the bees in the Black Beauty was lower than in the Early Long Purple. In the Early Long Purple, *X. caffra* had a PE of 3.447 while in the Black Beauty its PE was 2.197. On the other hand the PE for *Nomia* sp. was 2.615 in the Early Long Purple while in the Black Beauty it lowered to 1.38 (table 19).

Bee species	Early long purple	Black beauty.
X. caffra	3.447	2.197
Nomia sp.	2.615	1.38

Table 19. Difference in PE of the bees in different eggplant cultivars.

3.5. The alternative forage resources of the eggplant pollinators.

3.5.1. Species composition of the alternative forage resources.

A number of plant species were noted as providing alternative forage to eggplant pollinators. These were:

1. *Duosperma kilimandscharicum* (Lindau) Dayton, Acanthaceae
2. *Justicia flava* Vahl, Acanthaceae
3. *Cordia sinensis* Lam., Boraginaceae
4. *Cadaba farinosa* Forrsk., Capparidaceae
5. *Acacia mellifera* (Vahl) Benth., Leguminoseae
6. *Cajanus cajan* (L.) Millsp. (pigeon pea) Leguminosea
7. *Tephrosia villosa* (L.) Pers., Leguminoseae.
8. *Commicarpus helenae* (J. A. Schultes) Meikle, Nyctaginaceae
9. *Solanum incanum* L., Solanaceae
10. *Grewia bicolor* Juss., Tiliaceae
11. *Lippia javanica* (Burm. f.) Spreng., Verbanaceae

12. *Balanites aegyptica* (L.) Del., Zygophyllaceae

3.5.2. Distribution of the alternative plant resources in the surrounding habitat

The plant species listed above were unequally distributed in the habitat surrounding the cropped land at Nguruman. This habitat comprised of open dry *Acacia* woodland, farmland, an *Acacia tortilis* riparian forest and a grassy sward. Of the 12 species 5 were found in the farm area, 5 in riparian forest, 3 in dry *Acacia* woodland and only 1 in grassland. The extent of each type of habitat along the transect and the plant species found in each habitat is shown in the table 3.

HABITAT	DISTANCE (Km).	% COVER OF HABITAT ALONG THE TRANSECT	PLANT SPECIES FOUND IN THE HABITAT.
Woodland	1.4	28	*A. mellifera, C. farinosa* and *B. aegyptica.*
Riparian forest	0.55	11	*S. incanum, T. villosa, G. bicolor, C. sinensis* and *L. javanica.*
Farmlands.	1.60	32	*S. incanum, C. helenae, J. flava, D. kimandscharicum* and *C. cajan.*
Grassland	1.45	29	*S. incanum.*

Table 20. The extent of habitats along the transect and the plant species constituting the alternative forage species.

The alternative forage found in the farm areas was mainly herbaceous and grew on the farm edges, fallow land and along footpaths. In the riparian forest they were mainly shrubs that grew along the river. In the woodland, *X. caffra* was seen going to the galls that formed on the leaves of *B. aegyptica*. The sap in these galls served as a food source.

Table 21 shows the seasonal change in the composition of the alternative forage.

Plant species	January	February	March.	May	June
A. mellifera	+	+	+	+	(+)
B. aegyptica	+	+	+	+	+
C. cajan	+	+	(+)	(+)	(+)
C. farinosa	+	+	+	+	(+)
C. helenae	(+)	(+)	(+)	(+)	(+)
C. sinensis	(+)	(+)	(+)	+	+
D. kilimandscharicum	(+)	(+)	(+)	+	+
G. bicolor	(+)	(+)	+	+	+
J. flava	(+)	(+)	(+)	(+)	(+)
L. javanica	+	(+)	(+)	+	+
T. villosa	(+)	(+)	+	+	(+)
S. incanum	(+)	(+)	(+)	(+)	(+)

Table 21. Seasonal change of alternative forage resources. (+) Means present and flowering, + means present but not flowering.

3.5.3. Pollinator preference among the alternative resources

Three plant species namely, *J. flava*, *C. helenae* and *D. kilimandscharicum* were visited by more pollinators as compared to other plants (figure 7). In all the plants , *X. caffra* was the most frequent visitor of all and in some plants such as *C. farinosa*, *A. mellifera*, *G. bicolor* and *B. aegyptica* it was the only visitor that was observed over the survey time.

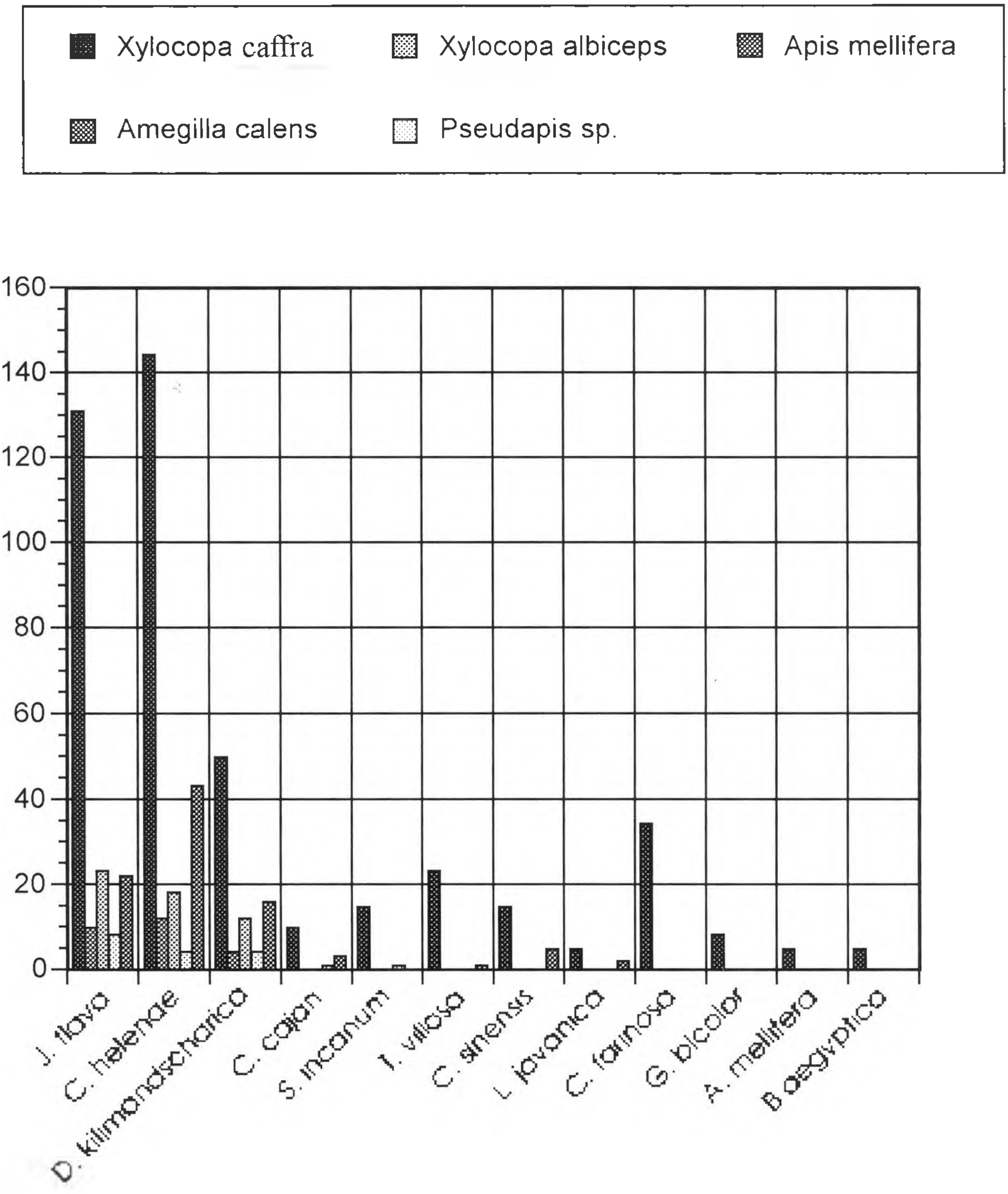

Figure 7. Frequency distribution of the bees on different plant species along the transect.

3.5.4. Distribution of the bees in the surrounding habitat

The distribution of the bees in the surrounding habitat was studied by comparing the % number of bees in each habitat to the percentage cover of the habitat along the transect. Naturally, if the bees were equally distributed in each of the habitats surrounding the farms, then their frequencies would be the same in all the habitats. The bees were not distributed equally in the surrounding habitats (table 22).

		January	February	March	may	June	Total	Average
Habitat type	Habitat cover (%)	Number of bees(%)	Number of bees(%)	Number of bees(%)	Number of bees(%)	Number of bees(%)		
Woodland	28	0	0	0	0	22.63	22.63	4.53
Forest	11	7.41	17.71	3.11	10	4.74	42.97	8.6
Farmland	32	91.11	81.77	94.94	86.67	67.89	422.38	84.48
Grassland	29	1.48	0.52	1.95	3.33	4.74	12.02	2.4

Table 22. Distribution of the bees in the surrounding habitats during the study period

There were more bees foraging the farmland than in any other habitat. The ratio of the % number of bees in each habitat to the % habitat cover (table 23) revealed that the bees foraged the farmlands more. The farmlands had a ratio of 2.65, the riparian forest 0.78, the woodland 0.16 and the grassland 0.08. The ratio in the farmland was greater than 1, showing that the bees preferentially foraged the farmlands (table 23 and figure 8).

		January	February	March	May	June	Total	Average
Habitat type	% of habitat	Ratio of % number bees : % habitat	Ratio of % number bees : % habitat	Ratio of % number bees : % habitat	Ratio of % number bees : % habitat	Ratio of % number bees : % habitat	Ratio of % number bees : % habitat	Ratio of % bees : % habitat
Woodland	28	0	0	0	0	0.8	0.8	0.16
Forest	11	0.674	1.61	0.28	0.91	0.43	3.904	0.78
Farmland	32	2.85	2.56	2.97	2.71	2.12	13.21	2.65
Grassland	29	0.051	0.02	0.07	0.11	0.16	0.411	0.08

Table 23. Habitat preference by the eggplant pollinators

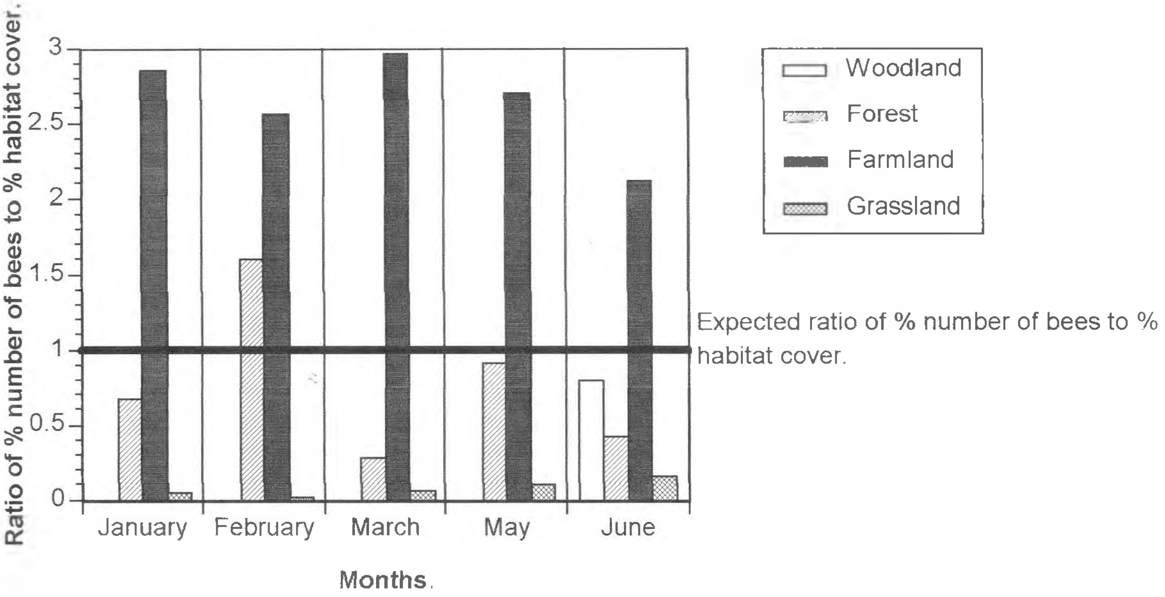

Figure 8. Distribution of the pollinators in the surrounding habitat during the study period

In the farmland there were bees foraging on the alternative plants all through the five-month period that the study was conducted. In the woodland, the bees were only present in June when the alternative forage plants in this habitat were flowering. There were bees in the riparian forest throughout the study period but it was foraged more in February than in the other months. The number of pollinators foraging the grassland was low throughout the study period.

The farm area had the most bees in terms of both species composition and species richness due to the constant occurrence of alternative forage plants species - *S. incanum, C. helenae, J. flava, D. kimandscharicum* and *C. cajan*. In other habitats, the alternative forage plants did not persist for long periods of time, making these habitats unreliable in terms of resource provisioning. Only three bee species namely, *A. mellifera, X. caffra* and the *X. albiceps* were encountered in the riparian forest. *X. caffra* was the only bee species to be found in both the open woodland and the grassy swards.

3.5.5. The relative abundance of the pollinators

The relative abundance of the pollinators in the surrounding habitat was calculated by dividing the total count of individual bees of each species by the total time (in hours) that was taken to survey the transect. The most abundant pollinator species in the area was *X. caffra*. The other pollinators (*A. mellifera*, *Pseudapis* sp., *A. calen*s and the *X. albiceps*) followed in a descending order. Table 7 illustrates the relative abundance of the pollinators.

Bee species	Number of bees	Time spent in the survey (hrs)	relative abundance (number of bees/ time spent)	% relative abundance
Xylocopa caffra	417	18.62	22.395	68.8
Apis mellifera	92	18.62	4.94	15.17
Pseudapis sp.	53	18.62	2.84	8.73
Amegilla calens	26	18.62	1.396	4.29
Xylocopa albiceps	18	18.62	0.967	2.97

Table 24. Relative abundance of the pollinators

CHAPTER 4

4.0 DISCUSSION

4.1 Floral and bee co-adaptation for buzz pollination

The eggplant is a very dependable source of pollen for the bees since it presents many flowers over a long period of time. It also produces several flowers in a day. However, the eggplant does not provide nectar to the pollinators and a complicated phenomenon arises in that while the pollinators need nectar, the eggplant provides pollen only and the pollen is not readily available since it requires vibration for its release. This is compensated for by the high nutritional value of the eggplant pollen.

All the eggplant pollinators were capable of effecting buzz-pollination except *A. mellifera*. Buzz pollinator bees are united by only one feature; the possession of well developed prothoracic muscles (Buchmann 1983). Three categories of visitation types have been described (Wille, 1963). The categories are (1) buzzing bees, (2) biting bees, and (3) gleaning bees. *A. mellifera* is an example of a gleaning bee that visits the eggplant. They move around the anthers and corollas, picking up pollen grains that fell before on the floral surface during previous buzzes by other bees. The honeybees could also have been attracted to the eggplant flowers by the pseudo-nectaries. Biting bees do great damage to the anthers by chewing them off in search of the hidden pollen. Examples of biting bees include some species of *Xylocopa* and *Trigona*. However, such bees were not observed on the eggplant flowers.

4.2. Reduction in yield due to insufficient pollination of the eggplant

In both cultivars of the eggplant, fruit set due to wind pollination was poor. No fruits were set in the Early Long Purple while only one fruit was set in the Black Beauty. Therefore, wind pollination is very ineffective in the pollination of the eggplant since the eggplant anthers are poricidal and pollen is not easily shed by wind.

Enhanced self-pollination experiments, done by applying pollen from the same flowers, showed that the eggplant is self-compatible, only that it requires an efficient means of pollination for high seed set to be achieved. Enhanced self-pollination resulted in high yields (mean seed sets = 928 in the Early Long Purple and 1935 in Black Beauty).

Seed set was highest in fruits resulting from enhanced cross-pollination (1227 in Early Long Purple and 2255 in Black Beauty) probably due to the timing of the treatments - pollen was applied on the 2nd day of flower opening when the stigmas were most receptive. Although open-pollinated flowers had a high seed set too, it was not as high as in fruits resulting from enhanced cross-pollination. High yield in the eggplant therefore relies on out-crossing which in nature can only be done by the pollinators.

The quality of the eggplant fruits was therefore greatly determined by the mode of pollination and loss of pollinators in the area can lead to a great reduction in the yield of the eggplant since wind is very ineffective and autogamy accounts for very little seed set

4.3. Visitation patterns of the eggplant pollinators.

4.3.1. Effects of time and temperature.

Time did not play any role in determining the total number of pollinators that were observed in the eggplant fields. However, the different bee species were active at different time periods , *A. calens*, *A. mellifera*, *Nomia* sp. and *X. caffra* were active between 06.30 a.m. and 11.30 a.m., but there frequencies were not the same in the different hourly time intervals. *X.albiceps*, *X. flavorufa*, and *Pseudapis* sp. were active after 07.30 a.m. and were present in the fields even after 12.30 p.m., though in low frequencies. The early activity of *X. caffra* and *Nomia* sp., which also happen to be most effective pollinators, enable them to get the maximum pollen reward from the eggplant, before the other bees deplete the pollen. This is also good for the plant in that its efficient pollinators visit the flowers when there is much pollen available for pollination.

Although time does not affect the number of flowers visited by bees, *X. caffra* visits more flowers that the other bees making it the most effective pollinator in terms of the high seed set obtained from flowers that it pollinates and the high number of flowers it pollinates.

The prevailing temperature and time of the day also play a role in determining other parameters that affect pollinators e.g., relative humidity, wind speed and light intensity.

4.3.2. Effect of resource abundance

In both eggplant cultivars, regression analyses showed that resource abundance did not affect the number of foraging pollinators in the fields or the number of flowers visited by each pollinator.

The finding that the number of pollinators foraging in the plots did not increase linearly with the resource abundance could be attributed to two factors. (1) Since the eggplant is a pollen only plant, pollinators have to allocate their foraging time between nectar plants and the eggplant, so pollinator frequency cannot increase indefinitely as the resource abundance increases. (2) The eggplant as a buzz-pollinated plant has co-evolved with its pollinators and since there are only a few buzz-pollinating species in the area the eggplant as a resource is not exploited to the maximum.

4.4. Pollinator effectiveness

The frequency at which the pollinators visited the eggplant fields changed with the seasons. In the first season, there were five pollinator species commonly observed in the Early Long Purple fields, of which was *Nomia* sp. was the most effective followed by the *Pseudapis* sp., *A. calens, X. caffra* and *A. mellifera.*

During the second growing season, only *X. caffra* and *Nomia* sp. occurred in high frequencies. *X. caffra* had the highest pollinator effectiveness at 3.447 while *Nomia* sp had a pollinator effectiveness of 2.615.

The pollinator effectiveness of these bees changed between the seasons. *X. caffra*'s efficacy increased from 0.217 to 3.447 and *Nomia* sp.'s efficacy increased from 1.331 to 2.615 in the second season.

The high pollinator effectiveness during the second growing season could be due to a general increase in yield during this season and the fact that young plants were used in the manipulations during the second season as compared to older plants that were used in the first growing season. The pollinator effectiveness of the pollinators in the Black Beauty was lower than in the Early Long Purple.

4.5 The spatial and temporal distribution of the eggplant pollinators and their alternative forage resource in the habitats around the farms

None of the 12 plant species that served as alternative forage to the eggplant pollinators was found in all the habitats that surrounded the farmlands. *S. incanum*, which is a wild relative of the eggplant, was found in 3 out of the 4 habitats that surrounded the farmlands and it was visited by only 2 out of the 11-pollinator species.

J. flava, C. helenae and *D. kilimandscharicum*, which were visited most by the pollinators, occurred mainly in the farmlands. *J. flava* and *C. helenae* flowered during the whole study period while *D. kilimandscharicum* was in blossom for 3 months (January, February and March). These 3 species served as the most important alternative resource for the eggplant pollinators.

In the riparian forest, there were 5 plant species that were visited by the pollinators, namely, *S. incanum, L. javanica, T. villosa, C. sinensis,* and *G. bicolor*. These plants only flowered for short periods of time as compared to the plants in the farmland. In the grassland *S. incanum* was the only alternative forage and it was visited by *X. caffra* only. The alternative forage resources in the woodland, *A. mellifera* and *C. farinosa* flowered only in June.

The bees foraged the farmland more as compared to the other habitats. The ratio of the % number of bees to the % cover of the habitat in the farmland averaged 2.65, showing that the bees preferentially foraged this habitat. All the pollinator species were present in this habitat.

The high number of pollinators that was observed in the farmland is possibly due to the constant occurrence of the most preferred alternative forage plants namely *J. flava, C.*

helenae and *D. kilimandscharicum*. *J. flava* and *C. helenae* flowered during the whole study period while *D. kilimandscharicum* was in blossom for 3 months (January, February and March).

The riparian forest had the next highest number of pollinators. The average ratio of the % number of pollinators to the % cover of the habitat averaged 0.78. This habitat was preferentially foraged in February when all the five alternative forage species in it were flowering and at this time, the ratio of the % number of pollinators to the % cover of the habitat was1.61.

In the grassland, the ratio of the % number of bees to the % cover of the habitat averaged 0.08, which was very low as compared to the farmland and the riparian forest. This habitat was the least rewarding and was not foraged much by the pollinators. In the woodland, where only 2 alternative forage species that flowered in June were recorded, the ratio of the % number of bees to the % habitat cover averaged 0.16. Only *X. caffra* foraged the plants in this habitat and they swarmed in large numbers over the trees. This is why although the trees flowered only in June, the woodland appeared more foraged by the pollinators than the grassland where *S. incanum* was flowering throughout the study.

An enquiry into the relative abundance of the bees based on their frequencies and the time spent in the study, showed that *X. caffra* was the most abundant pollinator species. It was present in all the habitats and visited all the flowering plants that were found in the habitat.

CHAPTER 5

5.0 CONCLUSION

The eggplant, though self-compatible, required efficient pollinators to vibrate the pollen out of the anthers so as to effect pollination. Both wind pollination and self-pollination were ineffective. *X. caffra* and *Nomia* sp. were determined to be the most frequent pollinators of the eggplant and were therefore responsible for pollination of the eggplant. These 2 bee species were capable of effecting buzz-pollination, a quality that made them capable of effecting pollination in the eggplant. The pollinator efficiency of the *X. caffra* was higher than that of *Nomia* sp. in both eggplant cultivars.

The prevailing ambient temperature affected the visitation patterns of the eggplant pollinators. Few pollinators foraged the fields at low temperatures. Likewise the number of flowers that the pollinators visited were few. As temperature rose, the number pollinators and the number of flowers they visited and increased.

The most important habitat for the pollinators in terms of the alternative forage resource is the farmland that comprises the farm edges, fallow land and the footpaths. The farmland is rich in the alternative forage plant species and should therefore be maintained.

The riparian forest, which is the habitat that is under immediate threat by the farmers, was also foraged much and should thus be maintained. The dead dry wood found in riparian forest is important as nesting sites for *X. caffra*. Clearing of the riparian forest which is mainly done by fires should therefore be checked so that the nesting sites for the most important pollinator (*X. caffra*) are not lost.

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