

Floral Biology, Breeding System, and Pollination Ecology of *Cucurbita moschata* (Duch. ex Lam) Duch. ex Poir. Varieties (Cucurbitaceae) from Parts of the Niger Delta, Nigeria

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Abstract: Flowering, breeding mechanisms, and pollination biology of *Cucurbita moschata* (Duch. ex Lam) Duch. ex Poir. varieties were studied. *C. moschata* carries male and female flowers on the same plant and is pollinated by thrips and bees with nectar and pollen as major rewards for the pollinators. Both flowers begin opening between 0330 and 0400 hours. The male flower opens for about 8 to 9 h and the female opens for 6 h 30 min to 7 h. There is, however, a period of overlap in the flower anthesis of both sexes, which coincides with the peak of pollen viability and pollinator activity. Pollen viability is about 90% in newly opened flowers but decreases to about 62% on closure and crashes to 8% after 1 day. Stigma receptivity, measured by pollen germination on the stigma, lasts from 1 day before anthesis to 2 days afterwards. There was no evidence of non-pseudogamous agamospermy.

Key Words: Breeding system, *Cucurbita moschata*, Cucurbitaceae, floral biology, Nigeria, pollination

Introduction

The family Cucurbitaceae, which consists of 2 subfamilies, Cucurbitoidae and Zanonioideae, is moderately large, consisting of about 130 genera and 900 species (Jeffrey, 1964, 1980). The species are distributed primarily in the warmer areas of the world, especially in the tropics and subtropics. They are less frequent in temperate regions because of their frost sensitivity (Tsuchiya & Gupta, 1991). The Cucurbitaceae, with about 21 genera and 41 species in Nigeria, have perhaps more species in cultivation than any other family. They are used for diverse purposes in different parts of the country, ranging from important items in the diet (vegetables) to occupying a special place in the life and culture of the many ethnic groups (Okoli, 1984). Three species of the genus *Cucurbita* L.—*C. moschata* (Duch. ex Lam.) Duch. ex Poir., *C. maxima* Duch. ex Lam., and *C. pepo* L.—occur in Nigeria and have been described by Hutchinson & Dalziel (1954), Purseglove (1968) and Agbagwa & Ndukwu (2004). The 'musk', *C. moschata*, is

rarely found growing in the wild; however, it occasionally grows as an escape on dumpsites in most parts of south-eastern Nigeria. It is cultivated in northern Nigeria for its fruit, and in southern Nigeria in a largely unimproved form 'ugboguru' cultivated for both the leaves and the fruit. While the leaves are important vegetables, the pulp of the fruit is also eaten when cooked (Okoli, 1984). Like the American species (Whitaker & Davis, 1962), Agbagwa and Ndukwu (2004) recognised and described 3 cultivars of *C. moschata* based on the fruit's morphological characteristics. Although these species play key roles as vegetables in Nigeria, studies on their pollination biology and breeding systems are lacking. More than half of the over 120 million people in Nigeria depend on this genus daily in one way or another as sources of vegetable supplement. This study describes the floral morphology, breeding, and pollination biology of the 3 varieties of *C. moschata*. The results will serve as a precursor for further research into the breeding and crop improvement strategies of this important vegetable crop.

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Materials and Methods

Source of Study Materials

The 3 fruit varieties of *C. moschata* used for the studies were sourced from local markets and subsistent farms in parts of the Niger Delta states of Akwa Ibom (Ikot Ekpene - 05°11'37"N, 07°42'36"E), Imo (Owerri - 05°29'27"N, 07°01'26"E), and Rivers (Ahoada - 05°04'58"N, 06°38'46"E; Rumuji - 04°56'19"N, 06°46'54"E; Etche - 05°00'42"N, 07°02'02"E). The fruits of the 3 varieties (Figure 1) are globose to slightly round and are 15-20 cm long and 10-12 cm in diameter. They are categorised into 3 varieties based on fruit colour and ornamentation (Agbagwa & Ndukwu, 2004): green, green with white smooth blotches, and green with punctate blotches.

Similar fruit varieties from different locations were pooled, the fruits sliced open, seeds scooped out and air dried for planting during the 2001 and 2002 planting seasons. From each variety, 50 plants were grown in March 2001 and monitored until August 2001 in the Botanical Garden of the University of Port Harcourt (04°54'10"N, 06°53'56"E), which is located in the humid rainforest of the Niger Delta, which has similar conditions to the localities from where the seed samples were collected. This was repeated within the same period in 2002. Observations were made on 10 plants of each variety chosen at random from the 50 plants for each year.



Figure 1. Fruit varieties of *C. moschata*. Letters A, B and C represent different fruit varieties.

Flower Morphology

Flower morphology was described using 10 inflorescences of each variety. The structure of the flowers, their position in the inflorescence, the morphology of the separate floral parts, and the possible effects they have on pollination and breeding strategies were assessed. Names of floral parts follow Radford et al. (1974) and Gill (1988).

Phenology

Observations of phenology of the different populations of the 3 varieties commenced at the beginning of flowering and continued until fruiting. Anthesis of the male and female inflorescences was monitored. The time of anthesis initiation and termination in flowers of each variety, flowering period of an inflorescence, and the entire flowering period of each variety were observed.

Pollen Viability

Pollen viability was tested by the lactophenol cotton blue method, which is fast and easy. Pollen grains were sampled at different hours of the morning (0700, 0800, 0900, 1000, 1100, 1200, 1400, and 1600 on 14 and 28 May and June and 14 July) and the day after the flowers closed. Pollen was dipped into a solution of lactophenol cotton blue in glass petri dishes for 5 min, then mounted on glass slides, and viewed under the light microscope. Deeply/completely stained pollens were considered viable.

Female Receptivity and Breeding System

Forty female flowers were enclosed in paper bags and mesh to keep away pollinators and prevent wind pollination. Twenty flowers were hand pollinated between 0700 and 0800 every day from 2 days before anthesis to 2 days after. Female receptivity was determined by observing pollen tube growth. Another 20 flowers were not pollinated in order to determine if fruit development occurs without pollination (agamospermy).

Flower Visitors/Pollination Ecology

Flower visitors were observed in the field and voucher specimens were collected with an insect net for identification at the Entomology Research Lab., Animal & Environmental Biology Dept., University of Port Harcourt. The frequency of visits, duration of each visit by an insect species, and insect behaviour while foraging for floral resources (nectar and pollen) were observed

and recorded. At different times during anthesis, 5 of each insect visitor were captured as they left a male flower and immobilised on a microscope slide. The number of pollen grains adhering to their bodies was counted using a stereomicroscope.

A population of *C. moschata* growing on an abandoned dumpsite in Choba village (Rivers State) and another in a subsistent farm in Emeabiam (Imo State) were observed during the same period in order to identify insect visitors and their behaviour. This was to determine if our experimental centre at the Botanical Garden, University of Port Harcourt, affected the natural visitors of this species in the wild or in farms.

Results

From germination through plant establishment to flowering, the 3 varieties were the same in terms of morphological characteristics. The inflorescences (male and female) in the 3 varieties were also the same with regard to morphology and phenological characteristics. Each fruit variety produced more than one type of fruit. Results compiled during the 2 years of investigation were similar and are reported below.

Habit, Flower Morphology, and Characteristics

The species is a profuse, annual herbaceous climber with a long-running vine, which is moderately strong and covered with coarse pilose hairs. They climb by means of severally coiled proximally trifid tendrils. The stem is moderately hard, hollowed, sharply or smoothly 5-angled, pilose on the ribs but glabrous in the grooves. The leaves are large (10-25 cm by 13-35 cm), cordate, shallowly 5-lobed, occasionally with white blotches and pilose (Figure 2).

Cucurbita moschata is monoecious with unisexual flowers. The flowers are acuminate in the bud, actinomorphic with a pentamerous perianth. The male flowers, which are more numerous and appear earlier than the female ones, are borne on a pedunculate raceme or sometimes solitary on a very long peduncle (Figure 2). The racemes bear about 10 to 15 flower buds, each with a tubular receptacle at the end of the pedicel. The 5 sepals are gamosepalous, acicular, hairy, deeply 5-lobed, and about 4.5 cm long. The 5 petals are gamopetalous, deeply 5-lobed, yellow, and pilose on both surfaces and inserted into the calyx-tube. The petals are campanulate, imbricate, and valvate. There are 3 (rarely 4)



Figure 2. *C. moschata* showing the cordate leaf and male flower. Arrow points to 2 thrips. Bar = 1 cm.

syngenesious stamens each with 15 folded anther-lobes (chambers), which open longitudinally. The female flower is always solitary with a short peduncle. There are 3 fused carpels, the ovary is inferior, unilocular, and parietal, with the placenta intruding deeply into the ovary thus making the chamber falsely trilocular. There are 3 forked stigmas on the style.

Pollen Viability

Pollen exposure and availability to insect visitors is within the period that the flowers are open. In newly opened flowers, pollen viability is about 96%. Upon closure, pollen viability is reduced to 78%-62%. Pollen viability was observed to decrease progressively from morning to afternoon and then rapidly decrease to about 8% after a day (Figure 3).

Flowering and Phenology/Anthesis

Flowering begins 8 weeks after planting with the male inflorescences emerging first and predominating in number all through the flowering period. The female inflorescence appears 3 weeks later. The ratio of male to female inflorescence per plant throughout the flowering period was about 9:1. The overall flowering period in the male inflorescence is 8 to 10 weeks and about 6 weeks in the female.

In both types of flowers, opening is initiated before dawn between 0330 and 0400. The anthers open before the male flowers have opened. Flowers in both sexes open by outward stretching of the corolla (Figure 4a and 4b) and close by wilting and spiral winding of the apical

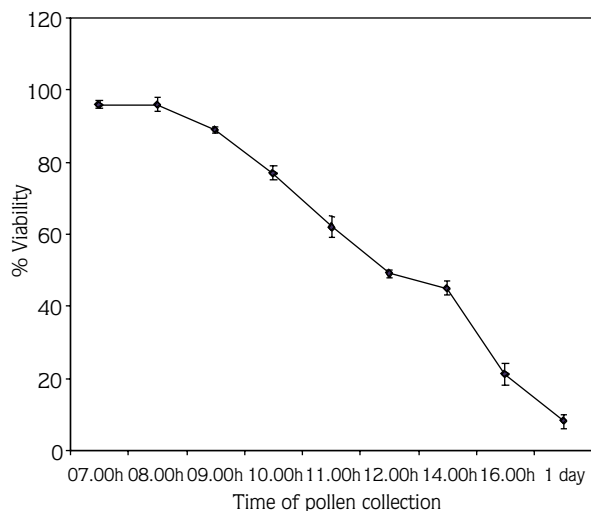


Figure 3. Mean pollen viability on observation days in May, June, and July 2001 and 2002.

part of the corolla (Figure 5). Full flower anthesis is attained between 0530 and 0600 in the male flowers (Figure 6) and between 0545 and 0700 in the female. Flower closure in both sexes is initiated at about 0900 of the same day. Final closure takes place between 1100 and 1200 in the male and about 1000 in the female. Flowers do not open again once closed. The duration of flower anthesis is about 2 h 30 min and 3 h 30 min in the male and female, respectively, whereas closure duration is about 3 h in the male and 1 h in the female. The male flowers open fully about 1 h before the female and close about 2 h after the female flowers.

Female Receptivity and Breeding System

Stigma receptivity, measured by pollen grain germination on the stigma, lasts from a day before anthesis to 2 days afterwards. This was observed in all samples treated. Over 70% of all hand-pollinated female flowers produced fruits. All bagged but non-pollinated female buds aborted. None developed into fruit.

Pollination and Pollination Mechanisms

Only 2 different species of flower-visiting insects were observed. They are small thrips (*Thysanoptera- Thrips* Haliday) and the honeybee (*Apis mellifera* L.). The 2 species exhibit different behavioural patterns. In addition to these species, *Acraea zetes* was observed on a population of *C. moschata* growing in a subsistent farm in Owerri Imo State. However, this species was observed to suck nectar with its proboscis with minimal contact with the pollen. It was not involved in pollinating activities.

The small thrips were regular visitors on *C. moschata* flowers. On each observation day, the thrips arrived at the flowers about the time of full flower anthesis between 0530 and 0600. They moved from the tip of the petals to the anthers (Figures 2, 4a and 4b) and down to the base of the campanulate petal, which is the nectar region or throat of the flower. At each time of observation, 3 to 5 thrips were seen foraging on 1 flower. The thrips are very slow in their foraging habit. Movement from the tip of the petal to the anthers and then to the nectar region for nectar feeding lasts between 2 and 6 h. Thrips spend a minimum of 2 h on 1 flower.

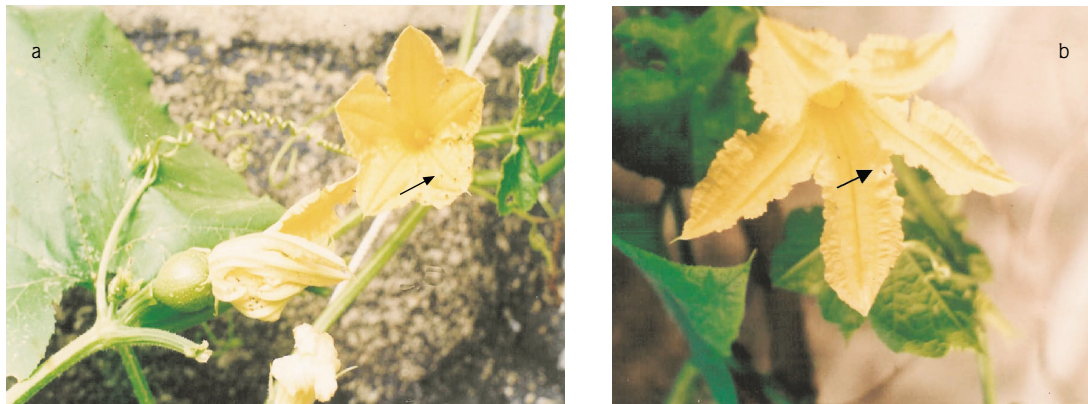


Figure 4a and b. Male and female flowers of *C. moschata* showing outward stretched corola. Arrow points to thrips. Bar = 1cm.



Figure 5. Showing spiral winding of *C. moschata* flowers. Bar = 1 cm.

After spending 45 min to 1 h in the nectar region of a flower, they move and land on the petals of another flower (whether male or female) on the same plant. On arrival, these thrips spend some time at the tip of the petal before moving on to the stigma or going down to the nectar region of the petal to forage for nectar. This

group of thrips leaves the flower before the sun becomes high. They are potential pollinators and represent about 30% of the total thrip visitors to the species. Another group of thrips (those that spend 6 h or more on 1 flower) does not move to any other flower. They spend most of the day inside one flower, going down into the base of the campanulate petal as the intensity of the sun gets stronger. This group, which represent about 70% of the thrips visitors, find their way out of the flower before the flower finally closes. All body parts of the thrip visitors were observed to carry pollen.

Apis mellifera (honey bee) starts visiting *C. moschata* flowers between 0630 and 0700. We observed 2 arrival or landing pathways for the bees. On male and female flowers, 1 approach is for the bee to land on 1 of the 5 petals and immediately fly to the anther or stigma. The other approach is for the bee to land directly on the anther or stigma. Whatever the approach, once a bee is on the anther or stigma, it adopts a supine feeding posture with the head oriented or positioned towards the campanulate nectar chamber or throat. The bee stretches out on the entire antheriferous column facing down towards the base of the column to get at the nectar. Occasionally, the bee pushes itself further down into the base of the corolla, moving around the chamber, and sucking/collecting nectar. After nectar feeding, the bee gradually withdraws from the chamber to its landing position on the anther or stigma and flies on to the next flower or away from the vicinity. On landing the hairs on the bee brush the anthers and pollen adheres to them. To put their head into the corolla chamber of the male flower, the bees align or appress their entire body firmly on the anthers. In this position the hairy ventral parts of the bees' body including the appendages carry a lot of pollen. When the bee exits from the male flower, it lands on the nearest leaf, waits a while, and removes some of

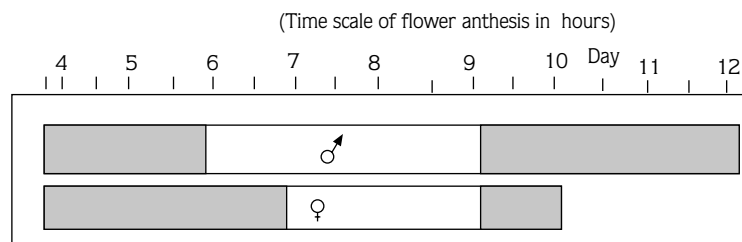


Figure 6. Time of opening and closing of male and female flowers during the flowering period in *C. moschata*.

the pollen with its leg and wing movement. Bee visits to male flower lasts 25 to 30 min. When a bee from a male flower lands on the petal or stigma of the female flower, pollen is deposited on the stigma on descent into the female flower. As the bee pushes down the stigma and moves around the circumference of the base of the stigma, it deposits more pollen. They were observed to spend 45 min to 1 h in a female flower.

Early bee visitors to male flowers were observed under the stereomicroscope to carry more pollen grains than later visitors.

Discussion

Floral Morphology and Phenology

Cucurbita moschata has monoecious, self-compatible unisexual flowers, which are actinomorphic with pentamerous perianths. Flowering in this species begins with opening of the male inflorescence followed by female flowers opening 2 to 3 weeks later. However, the male flower predominated throughout the experimental period with a ratio of 9:1 male to female flowers per plant. This observation is contrary to the findings published by Nepi and Pacini (1993) on *C. pepo*, where early formation of male flowers was reported with the female predominating afterwards. The brilliant yellow petals of both flowers attract pollinators. Although flowering in male and female inflorescences began at different times, the peaks of flowering in both sexes almost overlapped, favouring female receptivity (Richards, 1986; Nepi & Pacini, 1993). *Cucurbita moschata* flowers that bloomed when inflorescences were 2 weeks old were usually bigger and produced more pollen and nectar, thus attracting more insect visitors. Incomplete opening, withering or shrivelling of flowers was common in the first week of flowering in both sexes. Fruit abortion was also common among inflorescences that developed at the early and later weeks of flowering. Tangmitcharoen & Owens (1997) suggested that pollination success might be greater in flowers developing early and during the peak of the flowering period than in those that develop at the end of the flowering season. This is obvious in *C. moschata*, where the peaks of male and female flowering almost coincide. The attractive bright yellow colour of the petals and the campanulate shape of the flowers favour insect pollination. The campanulate throat provides shade for thrips on sunny days.

The beginning of anthesis is marked by the opening of the flower, irrespective of the type of pollination. The end of anthesis, on the other hand, occurs with the closing of the flower, ending pollen viability and stigma receptivity. Closing of the flower in *C. moschata* occurs when the pollen viability and stigma receptivity is decreasing. Nepi and Pacini (1993) similarly observed this in *C. pepo*. In *C. moschata*, there is a decrease in pollen viability beginning from 0700 on the day of opening. Even if the male flower remained open the next day, viable pollen capable of fertilising the ovules was not available. It is noteworthy that appreciable overlap in anthesis occurs between the sexes, but also there exists a period of about 30 min to 1 h during full flower anthesis that is out of phase. This scenario, which was observed by Nepi & Pacini (1993) in *C. pepo*, favours cross-pollination, especially at the beginning and end of anthesis.

The studies by Kerhoas et al. (1986) and Nepi & Pacini (1993) show that pollen grains of *C. pepo* lose so much water when exposed that viability suffers; this probably depends on the fact that, unlike most pollen, it does not dehydrate before anthesis and is therefore very vulnerable. This observation on *C. pepo* is similar to ours on *C. moschata*, where pollen grains are highly viable at first, but progressively decrease from 96% to about 8% 1 day after anthesis. The failure of pollen germination on the stigma after 5 min of pollination is associated with high sensitivity to dehydration (Nepi & Pacini, 1993) in *C. pepo*. Thus while the pollen is generally viable between 0700 and 1000 on observation days, pollen released on the stigma must achieve pollination within the first 5 min or becomes non-viable. By contrast, the pollen of *Eucalyptus rhodantha* Blakely & Steedm. is very resistant to different types of stress and its germination rate decreases by only a third after heating to 60 °C for 24 h (Heslop-Harrison & Heslop-Harrison, 1985).

Pollinators and Pollination Ecology

Faegri and Pijl (1979) suggested that in insect-pollinated plants nectar and pollen are the major rewards and are presented only at certain times. While this appears true for *C. moschata*, it is likely that nectar is the chief attractant due to a slight sweet scent that it exudes and the fact that nectar is produced in quantity over a long period. Insects that are primarily pollen collectors are usually thought to be more effective pollinators than those that are nectar collectors (Jay, 1986; Tangmitcharoen & Owens, 1997). Both insects observed on *C. moschata* during our field investigations (i.e. thrips and *Apis mellifera*) have been previously reported as good

pollen collectors and, as such, effective pollinators (Philippe, 1991; Nepi & Pacini, 1993; Endress, 1994; Ma et al., 1997; Tangmitcharoen & Owens, 1997; Luo & Li, 1999). In regularity and abundance, we observed that thrips occurred more than *Apis mellifera* on *C. moschata* flowers although both are effective pollinators. The fact that thrips carry large pollen loads was previously demonstrated by Luo & Li (1999) and Ma et al. (1997) on *Chloranthus Swartz* species. We also observed that the entire body of the insects collected from *C. moschata* flowers was covered with pollen grains. Endress (1994) summarised the features of flowers adapted to pollination by thrips and suggested that flowers that provide shelter together with a narrow entrance towards the floral centre are favoured by thrips. In addition, Luo & Li (1999) recognised scent and showy bright flowers as attractive to thrips, especially when combined. It is noteworthy that these characters outlined by Endress (1994) and Luo & Li (1999) are conspicuously present in *C. moschata* and most Cucurbitaceous species. As was observed, the second group of thrips that spend 6 h or more on one flower do not leave the flower until closure. These were observed to feed on the pollen and nectar of the flower as well as to shelter in the campanulate base of the *C. moschata* flowers. Thus, the thrips are first attracted by the bright yellow and scented petals of *C. moschata*, then feed on the abundant nectar and pollen, and finally receive shelter from the day's sunlight. Although this group of thrips carries abundant pollen, the first group that fly off to other flowers before the sun becomes intense are the potential pollinators.

Bees play an essential role in the pollination of *C. moschata* as in most Cucurbitaceae (McGregor & Todd, 1952; Robinson et al., 1989; Philippe, 1991; Nepi & Pacini, 1993). The arrival of these solitary bees on *C. moschata* flowers almost coincides with the resumption of early morning sun and opening of both male and female flowers. This also corresponds to the hours of peak pollinator activity, pollen viability, and decreases in the heat of the day. In this way, a high percentage of germination is assured, a fact that has been previously observed (Gould & Gould, 1988; Nepi & Pacini, 1993). The most efficient visits are the first ones because they result in the deposition on the stigma of a large number of highly viable grains. The floral size and architecture of *C. moschata*, i.e. the large petals (7 to 12 cm long) with campanulate shape, provide suitable landing platforms for

the bees. The slightly scented, bright yellow flowers attract the bees, especially under sunny conditions, when the scent is dispersed far away by solar radiation. All the bees captured had abundant pollen, mostly on their appendages and ventral body parts. The floral structure promotes access to pollen and restricts access to the nectar. Thus, for the solitary bees to gain access to the pollen, much effort is made to push backward and forward until they get into the nectar chamber. The bees suck the nectar in the chamber by circling the nectar receptacle. Although the female flowers are fewer, they were visited more often than the male flowers. A similar observation has been made on *C. pepo* (Couto et al., 1990; Nepi & Pacini, 1993) and *Cucumis melo* (Celli & Giordani, 1981). These authors opined that the female flowers probably produce more concentrated nectar than the male flowers. Thus, the quantitative and qualitative differences in nectar produced by both sexes ensure that the female flowers are adequately visited, although they are fewer. Nepi & Pacini (1993) therefore reasoned that the longer time it takes a bee to visit a female flower, as we also observed in *C. moschata*, is a function of the position of the nectar and its quantity.

Faegri and Pijl (1979) suggested that, in insect-pollinated plants, nectar and pollen are the major rewards and are presented only at certain times. This appears true for *C. moschata*. The slight scent that comes from the nectar of *C. moschata* suggests that nectar is the chief attractant. More likely, the large volume of nectar production in the female flowers necessitates longer stays of bees. However, the large quantities of pollen on the body parts of the bees imply that they are good pollinators. Insects that are primarily pollen collectors are usually thought to be more effective pollinators than those that are nectar collectors (Jay, 1986). However, nectar foragers have been found to be effective pollinators in almond orchards (Estes et al., 1983). This is the case with honeybees on *C. moschata*. The bees are both efficient in pollination, as demonstrated by the large quantity of pollen they carry, and also good foragers as observed in this study.

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