



Entomophily, ornithophily and anemochory in the self-incompatible *Boswellia ovalifoliolata* Bal. & Henry (Burseraceae), an endemic and endangered medicinally important tree species

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Abstract: *Boswellia ovalifoliolata* (Burseraceae) is a narrow endemic and endangered deciduous tree species. Its flowering, fruiting and seed dispersal events occur in a leafless state during the dry season. The flowers are small, bisexual, mildly odoriferous and actinomorphic; weakly protandrous but strictly self-incompatible. While insects and sunbirds pollinate the flowers, floral characteristics suggest that entomophily is the principal mode. Both bud and flower feeding by a weevil and flower and fruit feeding by the Palm Squirrel have been found to affect the success of sexual reproduction. The Garden Lizard serves as a predator of pollinating insects, especially bees and wasps, thus influencing pollination of this tree species. Fruit set in open pollination is below 10%, rising to 34% in manual cross-pollination. Limitation of cross-pollination, space constraints for seed production from all flower ovules and availability of limited resources in rocky, dry litter of the forest floor appear to constrain higher fruit set. Mature fruits dehisce and disseminate their lightweight, papery winged seeds with the aid of wind. The study site being windy provides the necessary driving force for effective dispersal of seeds away from parent trees. Seed germination occurs following rainfall but further growth depends on soil water and nutritional status. The success rate of seedling recruitment is highly limited, and it could be due to nutrient-poor soil and water stress resulting from dry spells during the rainy season.

Keywords: Anemochory, *Boswellia ovalifoliolata*, entomophily, ornithophily, self-incompatibility.

INTRODUCTION

The genus *Boswellia* belongs to the Burseraceae family and is widely distributed in the dry regions of tropical Africa, Arabia and India. In Africa, it is distributed in Somalia, Ethiopia, Eritrea, Kenya, Sudan, Tanzania, Madagascar and some other countries. In Arabia, it is mainly restricted to Yemen, Oman and Socotra. In India, it is distributed in a few regions such as Rajasthan, southeast Punjab, Danwara, Madras, etc. There are about 18 species of *Boswellia* which are shrubs or trees with outer bark often flaking. They include *B. sacra*, *B. frereana*, *B. neglecta*, *B. microphylla*, *B. papyrifera*, *B. ogadensis*, *B. pirottae*, *B. rivae*, *B. madagascariensis*, *B. socotrana*, *B. popoviana*, *B. nana*, *B. ameero*, *B. bullata*, *B. dioscoridis*, *B. elongata*, *B. serrata* and *B. ovalifoliolata*. Only the last two species have been reported to be distributed in India (Arabia 2005; Latheef et al. 2008). Sunnichan et al. (2005) mentioned that *B. serrata* is the only species found in India. But, other workers reported that *B. ovalifoliolata* occurs on the foothills of the Seshachalam hill ranges of Eastern Ghats in Chittoor, Cuddapah and Kurnool districts of Andhra Pradesh up to an altitude of about 600–900 m. It is a globally endangered, strict endemic

medium-sized deciduous medicinally important tree species and listed in CITES Red Data book under medicinal plants (Rani & Pullaiah 2002; Reddy et al. 2002). Chetty et al. (2002) reported that both *B. serrata* and *B. ovalifoliolata* occur at the foothills of Seshachalam hill ranges of Eastern Ghats.

Reproductive biology information is available for only a few species of Burseraceae such as *Commiphora weightii*, *Bursera medranoana*, *Sentiria laevigata* and *Boswellia serrata* (Sunnichan et al. 2005). *Boswellia ovalifoliolata* has not been investigated for its reproductive biology despite its medicinal importance in India. Our field surveys in the areas of Tirumala Hills have shown that the local tribes and others make deep incisions on the main trunk to extract the gum and resin, causing damage to trees which leads to population depletion. The gum is used to treat a number of conditions including ulcers, fever, stomach pain, scorpion sting, amoebic dysentery and hydrocele, while bark decoction is used for joint and rheumatic pains (Henry 2006; Latheef et al. 2008). We have investigated the floral biology, breeding behaviour, pollination and foraging behavior of pollinators of *B. ovalifoliolata* in its natural area, and the observations and results obtained are discussed in the light of the existing relevant information.

MATERIALS AND METHODS

Study area

The study area included Kapilatheertham and Deer Park areas of Tirumala Hills (13°42'N & 79°20'E, elevation 751m) of the southern Eastern Ghats in Andhra Pradesh. The approximate number of trees of *Boswellia ovalifoliolata* was 150 at Kapilatheertham and 60 at Deer Park. The trees occur mostly as small clusters at the former area while they are mostly scattered at the latter area. In both areas, the associated tree species are almost same and they include *Zizyphus rugosa* (Rhamnaceae), *Erythroxylum monogynum* (Erythroxylaceae), *Spondias pinnata*, *Buchanania axillaris* (Anacardiaceae), *Gyrocarpus asiaticus* (Hernandiaceae), *Dalbergia paniculata* (Fabaceae), *Schleichera oleosa* (Sapindaceae), *Ochna obtusata* (Ochnaceae), *Hugonia mystax* (Linaceae), *Ficus mollis* (Moraceae) and *Azadirachta indica* (Meliaceae). Of these, only the last one blooms during the flowering

season of *B. ovalifoliolata*. The floor of the area is completely dry with exposed rocks during summer but it is covered with luxuriant growth of herbaceous flora and grasses during rainy season. The field studies were carried out on the flowering season, floral biology, foraging activity, behavior and pollination by pollinators, and fruit, seed and seedling aspects of *B. ovalifoliolata* during 2007–2010.

Floral biology

The overall timing of leaf fall, leaf flushing, flowering and fruiting events was recorded. The number of flowers per inflorescence (N = 20) was recorded for 10 selected inflorescences, two each from five trees. These inflorescences were simultaneously followed for their flowering duration. The floral characteristics were recorded from 25 flowers collected from five each from five trees. Mature flower buds on ten inflorescences were tagged and followed for recording the time of flower opening. The same flowers were followed for recording the time of anther dehiscence. The pollen grain characteristics were recorded by consulting the book of Bhattacharya et al. (2006). Pollen production per flower was calculated following the method described by Cruden (1977). Pollen fertility was assessed by staining them in 1% acetocarmine. Stigma receptivity and nectar volume, sugar concentration and sugar types were assessed by following the methods prescribed by Dafni et al. (2005).

Breeding behavior

Fifty mature buds, five each from 10 inflorescences on five trees were bagged a day before anthesis without manual self pollination to know whether fruit set occurs through autogamy. Another set of 50 mature buds was selected in the same way, then emasculated and bagged a day prior to anthesis. The next day, the bags were removed and the stigmas were brushed with the freshly dehisced anthers from the flowers of the same tree and re-bagged to know whether fruit set occurs through geitonogamy. Ten trees were selected for manual cross-pollination and open-pollination. One hundred and twenty five flowers were used per each tree for manual cross-pollination. For this, mature buds were emasculated and bagged a day prior to anthesis. The next day, the bags were removed; freshly dehisced anthers from flowers of another

tree were brushed on the stigma and re-bagged. Ten inflorescences on each tree were tagged and followed for fruit set in open-pollination (Sunnichan et al. 2005). The length of time followed for each of these breeding systems was six weeks. Twenty stigmas, four each from five trees were removed at 1500h and observed under the microscope for the number of pollen grains deposited by pollen vectors. The per cent of flower predation by an unidentified weevil was calculated by counting the number of damaged flowers on 50 selected inflorescences on 10 trees.

Foraging behavior of pollinators and pollination

Preliminary investigations on foraging activity were made at different times of the day including dawn and dusk. Based on this information, the number of foraging visits made by each species was made for 15 minutes in each hour during the entire period of the day. This data was used to calculate the total number of foraging visits made by each species for the entire day and also to calculate the total number of foraging visits made by each category of foragers in order to evaluate their relative importance and role in effecting pollination. The forage collected and the area of contact of the species with the floral sex organs were also observed to understand their role in pollination. Binoculars were specially used for this purpose.

Fruit, seed and seedling ecology

Field observations on fruit, seed and seedling ecology were also made to the extent possible due to certain restrictions in the study areas.

RESULTS

Floral biology

In *B. ovalifoliolata* (Image 1a), leaf shedding occurs during December–February, and flowering from first week of March to second week of April at population level. An individual tree flowers for about three weeks only. Leaf flushing occurs from the three week of April and continues through rainy season. In a few trees, flowering occurs before the fall of old leaves but complete leaf shedding occurs when flowering is at its peak. The leaves are imparipinnate and crowded at the ends of branches. The flowers are borne in branched panicles at the ends of the branches (Image

1b). Each branch produces 8–10 inflorescences and each inflorescence produces 35.2 ± 13.77 (Range 16–72) flowers over a period of 5–14 days. The flowers are pedicellate, greenish-white, 6mm long, 5mm across, mildly fragrant, cup-shaped, bisexual and actinomorphic. The sepals are five, minute, basally connate, imbricate, light green, lightly pubescent outside and persistent without any further growth during post-fertilization stage in fruited flowers. The petals are five, white, free, imbricate, 5mm long and erect. Stamens are inserted outside a fleshy annular pinkish-red nectary disc which is present outside the ovary at the flower base. They are 10 arranged in two whorls, each with 2mm long white filament and 1mm long dorsifixed yellow dithecal anther (Image 1c). The pistil is clearly distinguished into ovary, style and stigma. The ovary is superior, trilobular, each locule with two pendulous ovules borne on axile placentation. The style is light pink at base and dark green above, 4mm long and trilobed. The stigma is short, capitate, shiny and wet papillate type (Image 1e,f).

The flowers open for a brief period daily during 1100–1300 hr. A fully open flower shows petals in erect position exposing the stamens and stigma. The stigma extends 1mm beyond the anthers and remains in that state throughout the flower's life. Anther dehiscence is nearly synchronous with flower opening. The anthers dehisce by longitudinal slits along the theca and release pollen grains. The pollen grains are light yellow, sticky, quadrangular, tricolporate with smooth exine and $66.4 \mu\text{m}$ in size (Image 1d). An anther produces 683.4 ± 40.97 (Range 602–748) pollen grains while the total pollen output per flower is 6834 of which 72% is fertile and the remaining is sterile. The fertile pollen to ovule ratio is 820.1:1. The stigma attains receptivity two hours after anthesis and remains receptive until the noon of the next day. A flower produces $0.4 \pm 0.15 \mu\text{l}$ of nectar with $53.8 \pm 1.75\%$ (51–56 %) sugar concentration. The nectar sugars include glucose, fructose and sucrose with the last as more dominant. The nectar also contains both essential and non-essential amino acids. The essential amino acids are arginine, histidine, lysine and threonine while the non-essential amino acids are alanine, aspartic acid, cysteine, glycine, hydroxyproline, serine, glutamic acid and tyrosine. The flowers drop off by the evening of the second day if not pollinated while only pistil and sepals remain intact in pollinated flowers.

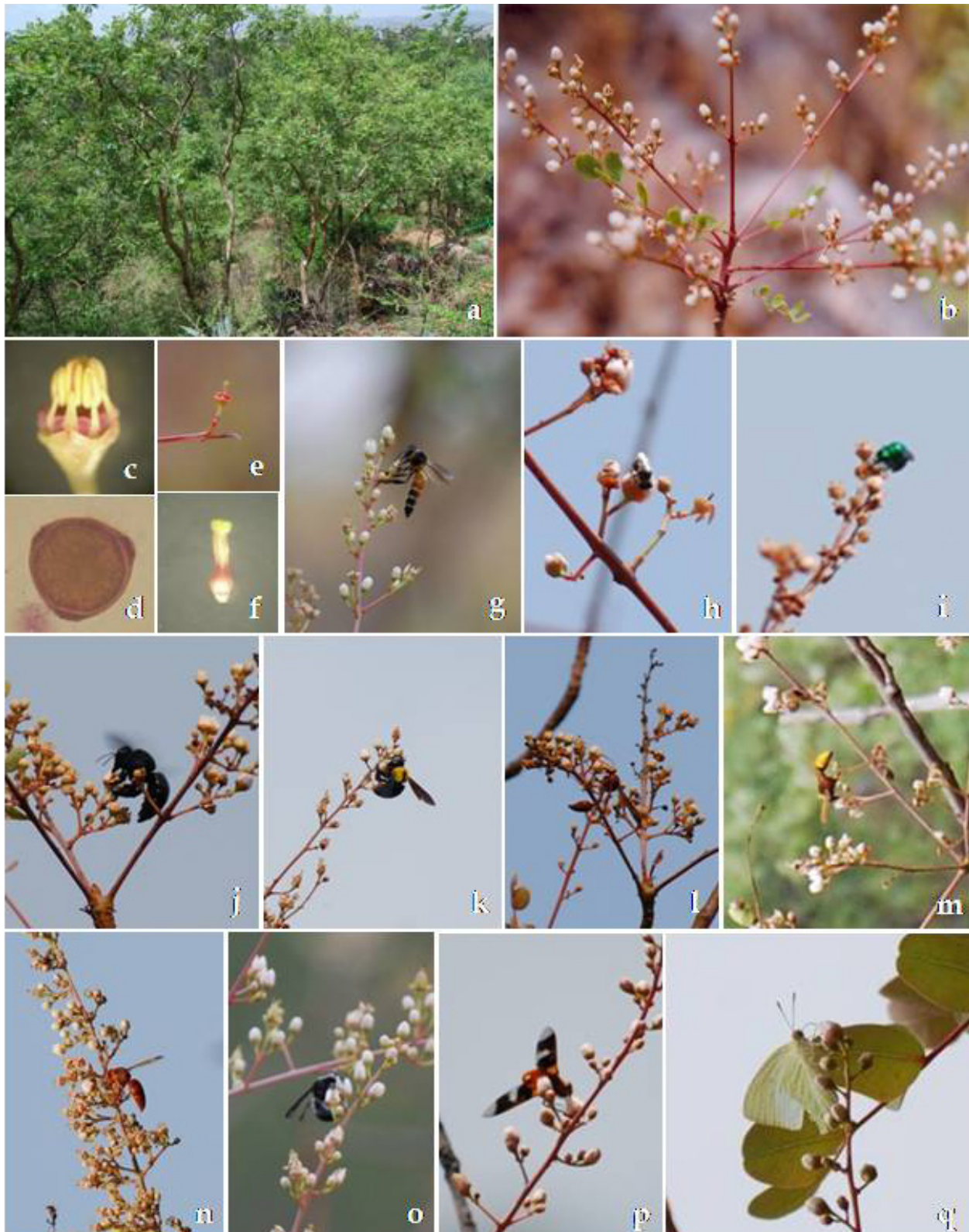


Image 1. *Boswellia ovalifoliolata*

a - Tree; b - Flowering inflorescence; c - Position of stamens; d - Pollen grain; e&f - Pistil; g - *Apis dorsata*; h - *Trigona iridipennis*, i - *Ceratina* sp.; j - *Xylocopa latipes*; k - *Xylocopa pubescens*; l - *Eumenes conica*; m - *Eumenes petiolata*; n - *Eumenes* sp.; o - *Rhynchium* sp.; p - *Hyperalonia* sp.; q - *Catopsilia pomona*.

Foraging activity and pollination

The flowers offer both pollen and nectar. They were foraged by insects and sunbirds during daytime throughout the flowering season. The insect foragers included bees, wasps, flies and butterflies. The bees included *Apis dorsata* (Image 1g), *A. cerana*, *A. florea*, *Trigona iridipennis* (Image 1h), *Ceratina* sp. (Image 1i), *Xylocopa latipes* (Image 1j) and *X. pubescens* (Image 1k). Juvenile *Xylocopa* bees were nectar foragers while all other bees were nectar and pollen foragers (Table 1). *Apis* and *Trigona* bees foraged throughout the day from 0700–1800 hr while the other bees during 0800–1300 hr (Fig. 1). The wasps included *Scolia* sp., *Rhynchium* sp. (Image 1o), *Eumenes* sp. (Image 1n), *Eumenes petiolata* (Image 1m) and *E. conica* (Image 1l). They were exclusively nectar foragers and their foraging visits were almost confined to 0800–1400 h (Fig. 2). The flies were represented by *Hyperalonia* sp. only (Image 1p); it collected only nectar during 0800–1200 hr (Fig. 3). Butterflies included four species - *Catopsilia pomona* (Image 1q), *Junonia lemonias* (Image 2a), *Acraea violae* (Image 2b,c) and *Danaus chrysippus* (Image 2d). They are nectar foragers and visited the flowers during 0800–1700 hr (Fig. 4). The sunbirds, *Nectarinia asiatica* (Image 2f,g) and *N. zeylonica* visited the flowers day long from 0700 to 1800 hr with more foraging activity during 1000-1300 hr (Fig. 5). Of the total insect and sunbird visits, bee visits constituted 62%, wasps 17%, sunbirds 12%, butterflies 7% and flies 2% (Fig. 6). Other passerine birds such as *Pycnonotus jocosus*, *P. cafer*, *Pericrocotus cinnamomeus*, *Dicrurus adsimilis*, *D. caerulescens*, *Parus xanthogenys*, *Turdoides striatus*, *Motacilla flava*, and a non-passerine bird, *Megalaima haemacephala* also visited the flowering trees in quest of nectar but discontinued flower-probing immediately (Table 1).

All insect categories after landing probed the flowers for nectar and/or pollen. The forehead and ventral surface of the body of the insects except butterflies were found to be contacting the anthers and stigma invariably while probing the flower for nectar. The bees while collecting pollen from the anthers normally contacted the stigma on their underside and hence were considered to be transferring pollen and effecting pollination. *Trigona* bees mostly forage on one tree largely effecting self-pollinations. *Apis*, *Ceratina* and juvenile *Xylocopa* bees made frequent inter-tree flights

Table 1. List of flower foragers on *Boswellia ovalifoliolata*

| Family | Scientific name | Common name |
|-----------------------------|---|-----------------------|
| Order: Hymenoptera | | |
| Apidae | <i>Apis dorsata</i> F. | Rock Bee |
| | <i>A. cerana</i> F. | Indian Honey Bee |
| | <i>A. florea</i> F. | Dwarf Honey Bee |
| | <i>Trigona iridipennis</i> Smith | Stingless Bee |
| | <i>Ceratina</i> sp. | Small Carpenter Bee |
| | <i>Xylocopa latipes</i> Drury | Large Carpenter Bee |
| | <i>X. pubescens</i> Spinola | Large Carpenter Bee |
| Scoliidae | <i>Scolia</i> sp. | Digger Wasp |
| Vespidae | <i>Eumenes petiolata</i> (F.) Smith | Potter Wasp |
| | <i>Rhynchium</i> sp. | Potter Wasp |
| Eumenidae | <i>Eumenes conica</i> F. | Potter Wasp |
| | <i>Eumenes</i> sp. | Potter Wasp |
| Diptera | | |
| Bombyliidae | <i>Hyperalonia</i> sp. | Pomace Fly |
| Lepidoptera | | |
| Pieridae | <i>Catopsilia pomona</i> F. | Common Emigrant |
| Nymphalidae | <i>Junonia lemonias</i> L. | Lemon Pansy |
| | <i>Acraea violae</i> F. | Tawny Coster |
| | <i>Danaus chrysippus</i> L. | Plain Tiger |
| Class: Aves | | |
| Order: Piciformes | | |
| Capitonidae | <i>Megalaima haemacephala</i> Status Muller | Coppersmith |
| Order: Passeriformes | | |
| Nectariniidae | <i>Nectarinia asiatica</i> Latham | Purple Sunbird |
| | <i>N. zeylonica</i> L. | Purple-Rumped Sunbird |
| Pycnonotidae | <i>Pycnonotus jocosus</i> L. | Red Whiskered Bulbul |
| | <i>P. cafer</i> L. | Red-Vented Bulbul |
| Campephagidae | <i>Pericrocotus cinnamomeus</i> L. | Small Minivet |
| Dicruridae | <i>Dicrurus adsimilis</i> Bechstein | Black Drongo |
| | <i>D. caerulescens</i> L. | White-Bellied Drongo |
| Paridae | <i>Parus xanthogenys</i> Vigors | Yellow-Cheeked Tit |
| Muscicapidae | <i>Turdoides striatus</i> Dumont | Jungle Babbler |
| Motacillidae | <i>Motacilla flava</i> L. | Yellow Wagtail |

in search of more forage. Wasps also exhibited similar foraging behaviour. The fly tended to forage mostly on the same tree collecting nectar very slowly from each flower. The butterflies made frequent inter-tree flights in quest of more nectar; they inserted proboscis through the stamens as well as from the sides of the petals for nectar collection. The Oriental Garden

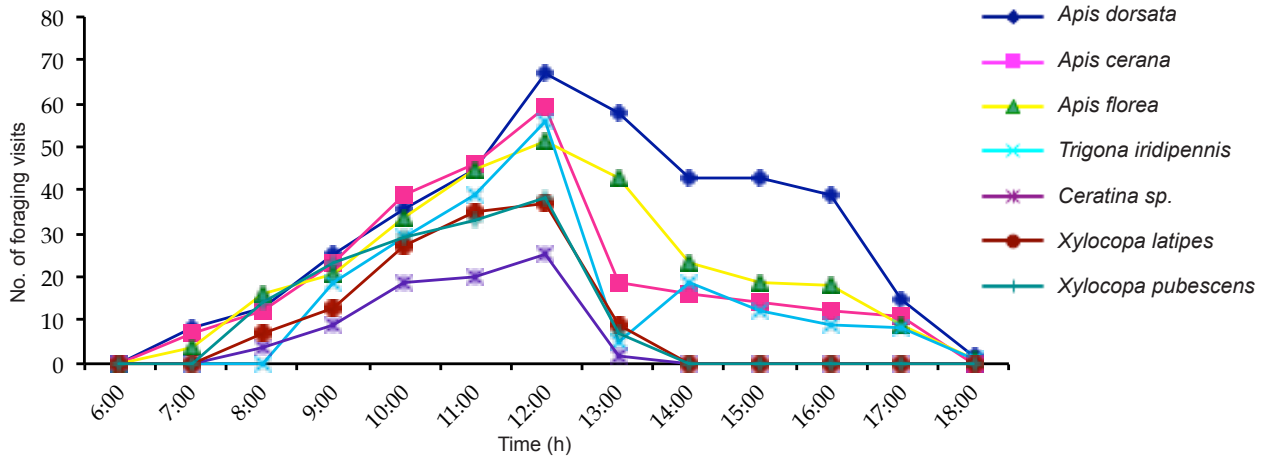


Figure 1. Hourly foraging activity of bees on *Boswellia ovalifoliolata*

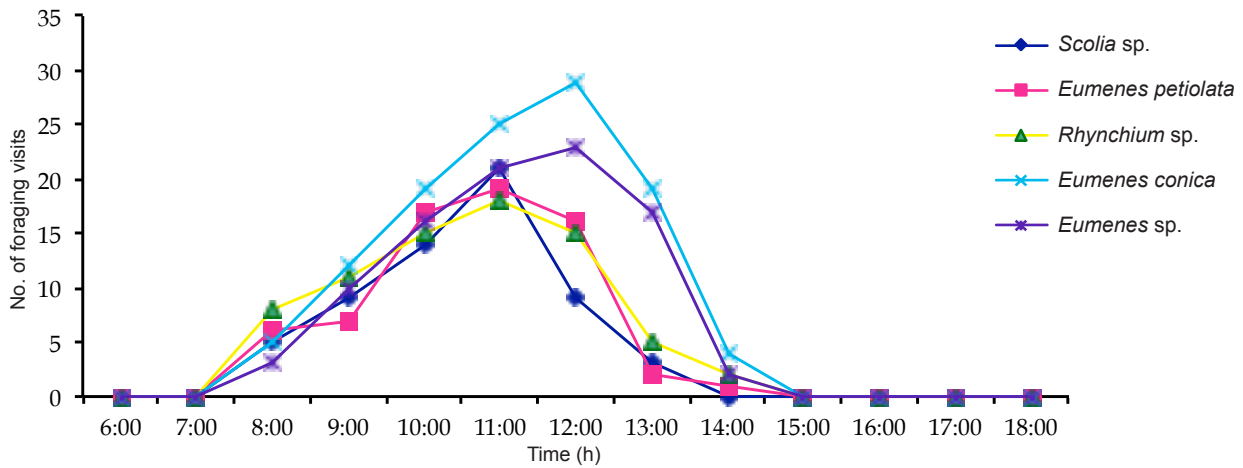


Figure 2. Hourly foraging activity of wasps on *Boswellia ovalifoliolata*

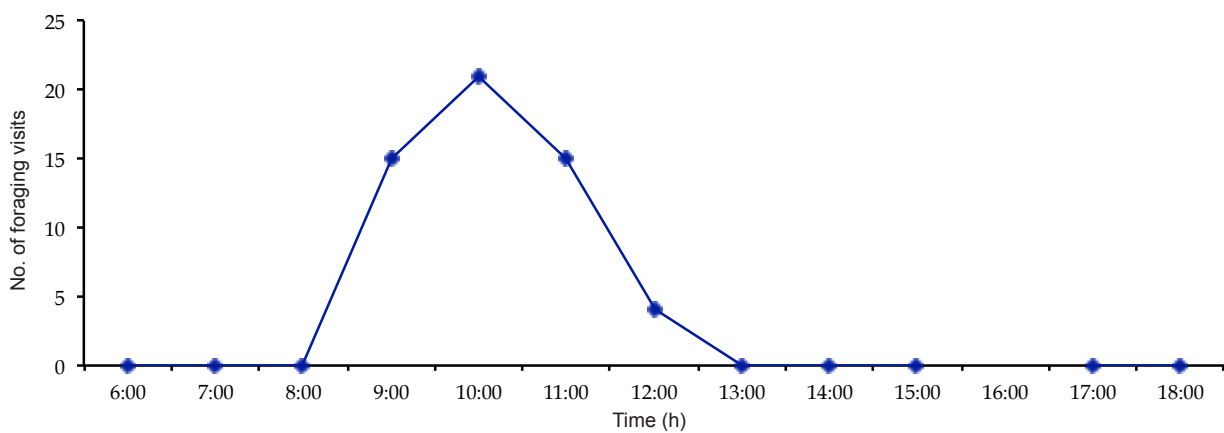


Figure 3. Hourly foraging activity of the Dipteran, *Hyperalonia sp.* on *Boswellia ovalifoliolata*

Lizard, *Calotes versicolor* (Squamata: Agamidae) was found to lie in wait closely to the flowers to capture the foraging insects (Image 2e). The prey species for

this lizard were mainly the foraging bees and wasps. Sunbirds landed on the inflorescence branches, walked to the flowers and inserting their curved beak to collect

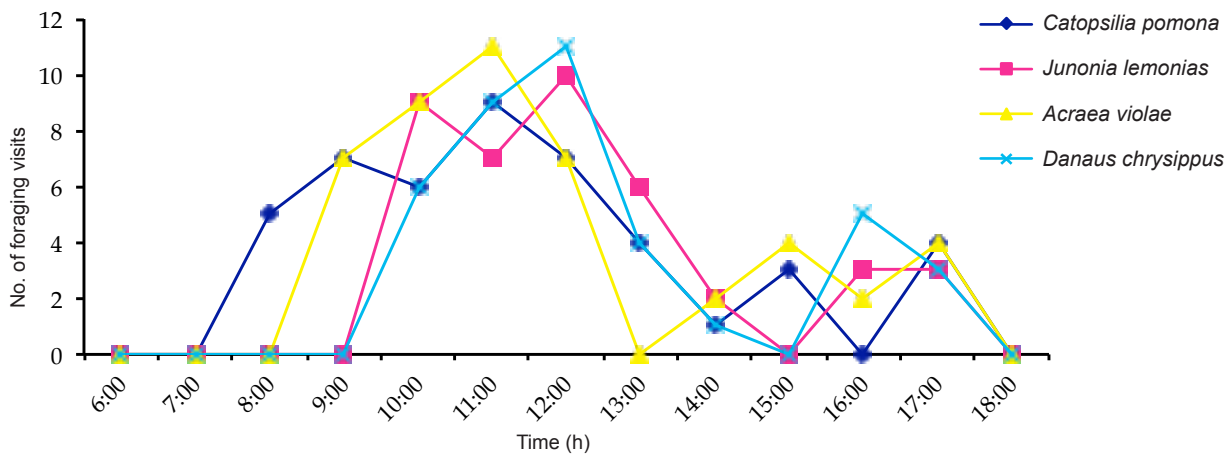


Figure 4. Hourly foraging activity of butterfly on *Boswellia ovalifoliolata*

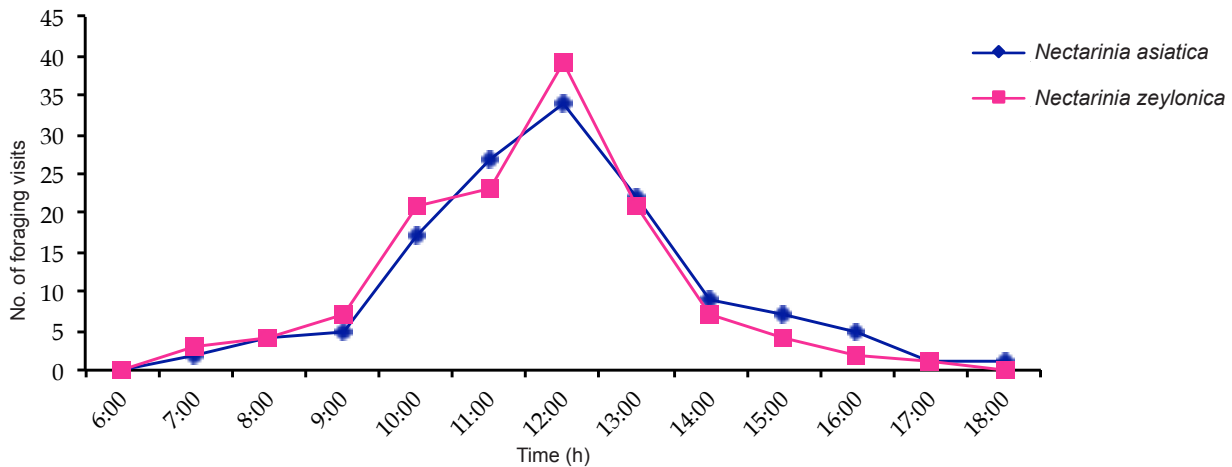


Figure 5. Hourly foraging activity of sunbirds on *Boswellia ovalifoliolata*

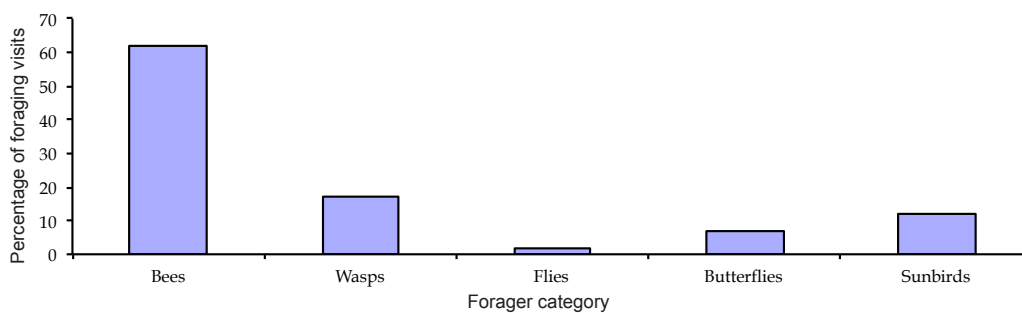


Figure 6. Relative percentage of foraging visits of different categories of insects and sunbirds on *Boswellia ovalifoliolata*

nectar; while doing so, the beak invariably contacted both the stigma and stamens and such a contact was considered to be transferring pollen and effecting pollination.

Breeding behavior

The inflorescences with mature buds when bagged without emasculation did not set any fruit. Further, the manual flower-to-flower selfing on certain inflorescences of the same tree also did not produce any fruit. In different trees, the fruit set varied from

Table 2. Fruit set under open pollination and manual xenogamous cross-pollinations on 10 selected trees of Tirumala Hill population

| Tree number | Per cent fruit set (open pollination)* | Per cent fruit set (hand cross-pollination)** |
|-------------|--|---|
| KT1 | 4.3 | 24.2 |
| KT2 | 9.8 | 12.0 |
| KT3 | 3.4 | 19.2 |
| KT4 | 2.4 | 19.0 |
| KT5 | 2.9 | 31.6 |
| DP1 | 4.1 | 26.4 |
| DP2 | 4.0 | 15.2 |
| DP3 | 1.8 | 16.8 |
| DP4 | 8.7 | 33.7 |
| DP5 | 4.1 | 10.8 |

KT - Kapilatheertham; DP - Deer Park; * - Average of 10 inflorescences per tree; ** - Average of 125 pollinations per tree.

10.8 to 33.7 % in manual cross-pollinations while it ranged from 1.8 to 9.8 % in open pollinations (Table 2). The results indicated that the site has no effect on fruit set rate from open or hand-cross pollinations. Further, the difference in fruit set rate in these two pollination modes is quite significant (Pearson's Correlation Coefficient 0.877). A weevil species was found feeding on buds and flowers (Image 2j,k); the percent of bud predation is 18% and that of flower predation is 27%. Further, Three-Striped Palm Squirrel *Funambulus palmarum* (Family: Sciuridae) was found to be feeding on flowers and fruits (Image 2h,i). The exact percentage of flowers and fruits fed could not be estimated due to difficulty in accessing the flowering branches and in following the feeding activity of the squirrel in the forest. But, visual observations indicated that the squirrel fed voraciously on flowers and growing fruits showing a significant effect on the reproductive success of the plant.

Fruit, seed and seedling ecology

Natural fruit set rate is 9.3 ± 4.63 (Range 2–24) at inflorescence level (Image 2l). The average flower to fruit ratio is 3.7: 1. The fruit is initially light green (Image 2m), then creamy white and light brown when mature. It grows to a maximum length of 13–14 mm and of 6mm width in four weeks. It is a simple septicidal trigonous capsule with a weight of 179 ± 26.6 mg and invariably produces three seeds against the actual six ovules in a flower. The ovule to seed ratio is

2:1. The seeds are winged, papery, compressed, 7mm long, 4mm wide and 19.9 ± 3.1 mg weight. The fruits dehisce along the septa to disseminate seeds into the air by the end of May (Image 2n,o). The seeds being light in weight disseminate easily by the wind. The study site is windy and the seeds travel distances up to 400m downhill. The seeds germinate following monsoon showers in June-July (Image 2p,q) but the success rate seemed to be dependant on the continuity of rain and the nutritional status of soil. Some seedlings were found to show symptoms of chlorosis which may be due to water and nutrient deficient soils in rocky habitats.

DISCUSSION

Boswellia ovalifoliolata is a deciduous tree species because it is leafless when in bloom. Leaf flushing occurs almost at the end of fruiting. In a few trees, leaf flushing is little bit early when fruits are still green and young. The short flowering period evidenced at individual as well as population level, massive blooming and the position of panicle inflorescences at the end of branches serve as a cue for foragers to collect floral rewards from the flowers. The floral characteristics of *B. ovalifoliolata*, such as fresh mild odour, hidden nectar in moderate quantity and pinkish-red nectary disc serving as nectar guide, conform to bee-flowers (Faegri & van der Pijl 1979). However, the small flower size, delicate petals and actinomorphic symmetry are not suitable for foraging visits by adult *Xylocopa* bees (Faegri & van der Pijl 1979), although the flowers can withstand juveniles. The observed *Xylocopa* bees are juveniles because they emerge from brood during March–April (Raju & Rao 2006) and hence they are suitable for probing the flowers to collect nectar. These juvenile bees in quest of nectar for instant energy and for overcoming dehydration make multiple visits to closely and distantly spaced flowering trees of *B. ovalifoliolata*. Such consistent flower visits between trees effect and enhance cross-pollination rate. *Apis*, *Trigona* and *Ceratina* bees collect pollen and nectar with ease due to cup-like flower shape with exposed floral rewards. Baker & Baker (1982; 1983) stated that short-tongued bees such as the bees observed in this study tend to be rewarded with sucrose-rich nectar. Further, Cruden et

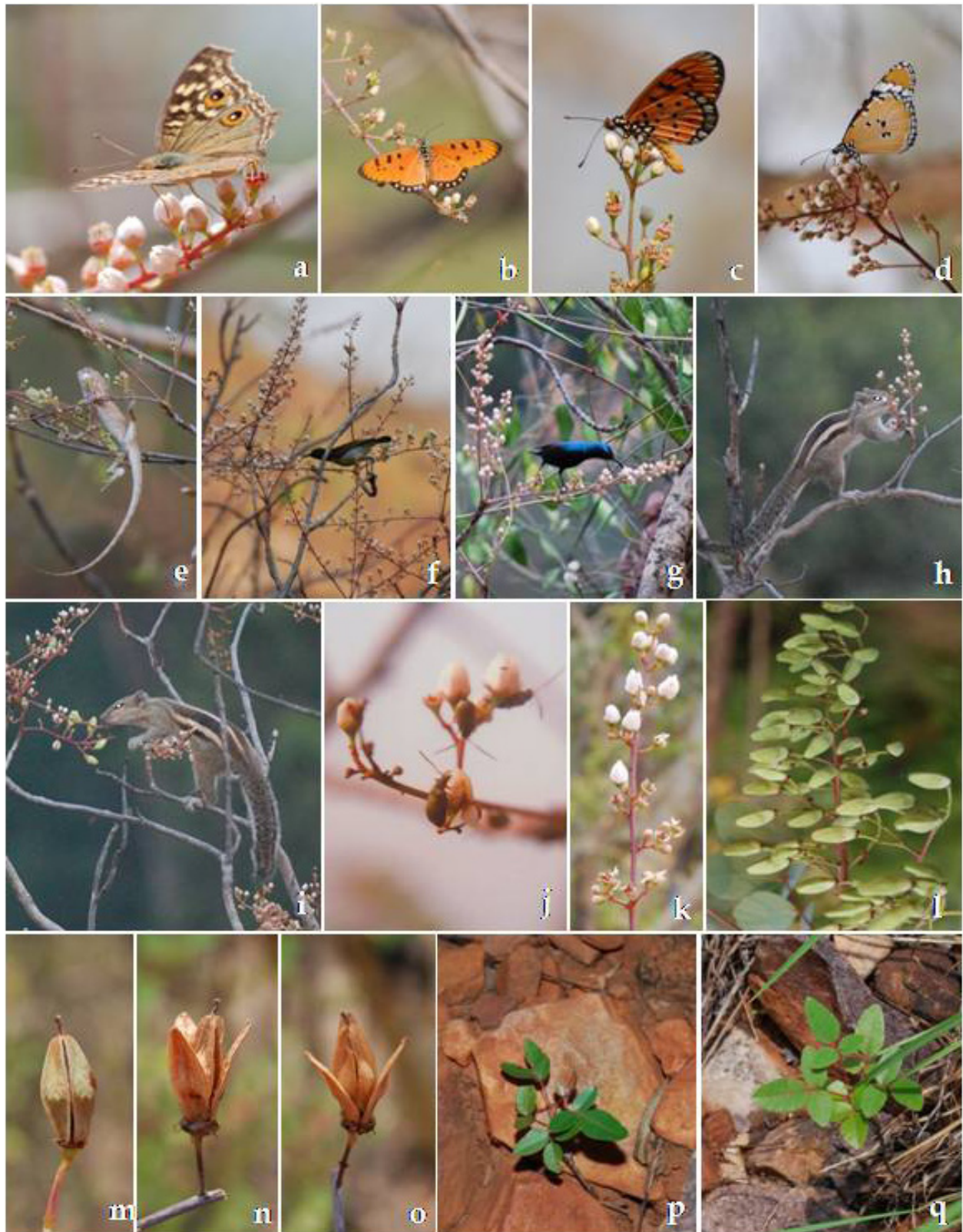


Image 2. *Boswellia ovalifoliolata*

a - *Junonia lemonias*; b&c - *Acraea violae*; d - *Danaus chrysippus*; e - *Calotes versicolor*; f&g - *Nectarinia asiatica* (male and female); h&i - *Funambulus palmarum* (flower and fruit feeding); j&k - Weevil feeding on buds and flowers; l - Fruit set; m - Maturing fruit; n&o - Fruit dehiscence; p&q - Healthy seedlings.

al. (1983) reported that in dry seasonal forest plants, the nectar concentration is usually high and bee-flowers produce a small volume of nectar with high sugar concentration. In *B. ovalifoliolata*, the flowers produce a small volume of sucrose-rich nectar with high sugar concentration and hence conform to the generalizations stated by Baker & Baker (1982; 1983) and Cruden et al. (1983). In line with this, bees recorded consistently visit the flowers of different trees to collect forage and in doing so effect pollination. *Apis dorsata* being a large-bodied bee requires more energy and hence efficiently probes the flowers in quick succession on the same and different trees; its foraging visits to different conspecific trees not only effect but also enhance cross-pollination rate. Other *Apis* species, *Ceratina* and *Trigona* bees with slow mobility between conspecific trees for forage collection mostly effect self-pollination which is not the mode of breeding system in *B. ovalifoliolata*. Hence, these bees have a minor role in cross-pollination. Wasps usually take nectar as a supplement food, especially when brood nursing is over. They are active in blossoms towards the end of flowering season in seasonal climates. Wasp-flowers are also sucrose-rich but are usually unreliable and unsteady pollinators (Faegri & van der Pijl 1979). The floral nectar of *B. ovalifoliolata* being sucrose-rich is favoured by the wasps, *Scolia*, *Eumenes* and *Rhynchium*. Their visits to the flowers throughout the flowering season suggests that their brood nursing period is over and hence, they are active in flowers to take nectar as a supplement diet. However, they are not consistent foragers like bees but they use this floral source until exhausted and their frequent inter-tree movement during their foraging period contributes to cross-pollination. The garden lizard is an ambush predator capturing the foraging insects at the flowers of *B. ovalifoliolata*. The foraging insects cannot perceive the lizard and do not respond by predator-avoidance behaviour. The lizard does not attack the prey until it forages on a flower for a considerable period. It is for this reason that the pollinator insects have greater opportunity of being approached and attacked by the lizard. The predation of the lizard on pollinating insects has its share in reducing the cross-pollination rate in *B. ovalifoliolata*. The role of dipteran fly in cross-pollination appears to be negligible due to its restricted inter-tree mobility. Butterfly-flowers also produce a small volume of sucrose-rich nectar with

high sugar concentration (Opler 1983; Cruden et al. 1983; Baker & Baker 1982; 1983). As the floral nectar of *B. ovalifoliolata* is characterized in this way, the foraging visits of the observed species of butterflies on this tree are not surprising. As they make frequent flights between trees, their foraging visits also contribute to cross-pollination. All these insect species carry considerable number of pollen grains on their body/proboscis, the character of which qualifies them as effective and efficient pollinators. The foraging activity of these insects coincides well with the timing of anthesis; it gradually increases from anthesis onwards, reaches to peak around noon and gradually decreases towards the evening. In *B. serrata*, honey bees have been reported to be the exclusive pollinators (Sunnichan et al. 2005).

Ornithophilous flowers tend to be large, red and deep seated with concealed nectar. They secrete high volumes of hexose-rich nectar with low sugar concentration (Cruden et al. 1983; Opler 1983; Baker & Baker 1990). On the contrary, in the present study, the sunbirds visit *B. ovalifoliolata* flowers which are small, cup-shaped and white with a small volume of sucrose-rich nectar with high sugar concentration. Since the nectar volume is very small and sunbirds require a greater amount of energy per flower, they visit different conspecific trees in quest of more nectar. Such a foraging behaviour results in cross-pollination. These sunbirds exhibit fidelity to this floral source until exhausted. Several other birds also attempt to collect nectar from *B. ovalifoliolata* but soon discontinue probing the flowers. The study shows that *B. ovalifoliolata* is not ornithophilous but sunbirds use it as nectar source for survival during dry season while other birds are unable to use it even in the absence of dry season blooming ornithophilous tree species in the study area. Therefore, the birds recorded in the study area appear to be searching for the floral nectar to meet their energy requirement during dry season.

Insects require ten essential amino acids but all of them are not normally found in all nectars. Usually, three to four essential amino acids and several non-essential amino acids are found in floral nectars (Baker & Baker 1982; 1983). Baker & Baker (1986) reported that the amino acids add taste to the floral nectar and it depends on their concentration. Their presence serves as an important cue for insects to visit flower and in the process effect pollination. In *B. ovalifoliolata*,

the nectar contains some essential and non-essential amino acids. Its nectar is an important source for four of the ten essential amino acids required by insects for their growth and development (DeGroot 1953). They include arginine, histidine, lysine and threonine. Non-essential amino acids are metabolized by insects from the food they take; however, floral nectar provides some of these amino acids instantaneously. The nectar of *B. ovalifoliolata* provides alanine, aspartic acid, cysteine, glycine, hydroxyproline, serine, glutamic acid and tyrosine. Therefore, the insects and also sunbirds by visiting and pollinating the flowers derive the dual benefit of sugars and amino acids from the nectar of *B. ovalifoliolata*.

In *B. ovalifoliolata*, the flowers are weakly protandrous, produce considerable per cent of sterile pollen and present the capitate, wet papillate trilobed stigma above the stamens as in case of its allied species *B. serrata* (Sunnichan et al. 2005). The stigma receptivity ceases around noon on the next day. These characteristics suggest that the tree species is adapted for cross-pollination which is further substantiated by the lack of fruit set in manual self-pollination treatments. The reason for the failure of fruit set in self-pollination appears to be related to inhibition of self-pollen tubes after their entry into the style. Therefore, the study suggests that *B. ovalifoliolata* is strictly self-incompatible and obligate outcrosser like *B. serrata* (Sunnichan et al. 2005). According to Cruden (1977), the pollen production rate at flower level is not commensurate with out-crossing breeding system but it seems to be appropriate if the fruit set rate in manual cross-pollination is considered. Fruit set in open-pollination among individual trees is less than 10% but it is most likely to increase in the absence of bud/flower predation by weevil and squirrel. The extent of increase in fruit set in manual cross-pollination also has not exceeded 34% and this suggests that there are inherent constraints such as dry conditions, nutrient-deficient environment to fruit set in addition to limitation of cross-pollination. The distribution of fruits on the inflorescence is sparse and hence, space is not a constraint for increased fruit set. As all fruits invariably produced three seeds, there seems to be a space constraint in the ovary for seed set from all six ovules of the flower. The uniform number of seeds in each fruit seems to be an evolved and adaptive trait to compensate the lower fruit set in open-pollinations.

It also suggests that cross-pollen availability is not a constraint in fruited flowers. In self-pollinated flowers, the deposited self pollen and the pollen tubes formed may prevent or block if the cross-pollen is subsequently deposited by insects/sunbirds. Further, the trees being leafless during the entire flowering and fruiting period have to utilize the available limited resources for fruit and seed loading. In consequence, the trees may even selectively disallow genetically inferior cross-pollinations to proceed further to set fruit in order to save available resources for pumping into the genetically superior fruits and seeds. The floor of the forest being rocky, dry and litter free during flowering and fruiting season deprives this tree species of nutrient resources. Therefore, *B. ovalifoliolata* with poor-nutrient environment is capable of performing reproductive events and produce some per cent of fruit set as a self-incompatible and obligate outcrosser. Similar reproductive events and constraints have been reported in *B. serrata* (Sunnichan et al. 2005). A recent experimental study with *Boswellia papyrifera* by Toon et al. (2006) shows that intensive tapping for gum causes the trees to divert too much carbohydrate into resin at the expense of reproductive organs, such as flowers, fruit and seeds. In consequence, the trees produce fewer smaller fruits with seeds of lower weight and reduced vitality than non-tapped trees. Such a situation in *B. ovalifoliolata* cannot be ruled out since it is an important source of gum resin for local tribes and hence there is a great threat to this globally endangered and endemic species.

Fruits mature in a short period and dehisce along the septa to disperse seeds for which dry conditions are essential. Their dispersal takes place in the month of May when temperature is at its maximum and which provides ideal conditions for seed dispersal by wind. The seed characteristics such as small size, light weight, papery and winged nature are adapted for anemochory. As the study site is windy, anemochory is very effective, dispersing seeds up to 400m away from the parental site. Therefore, in *B. ovalifoliolata*, dry season seems to be the prerequisite for flowering, fruiting and seed dispersal. Leaf flushing occurs immediately after seed dispersal and the water stress is released by rainfall in June and thereafter. During this period, with foliage, the tree has to produce and store the required energy for the recurrence of sexual reproduction in the next dry season. The dispersed

seeds germinate readily following rainfall but their continued growth and development is related to soil water and nutritional status. Since the natural area of *B. ovalifoliolata* is rocky with little litter and soil moisture, the success rate of seedlings each year is very much limited and hence, this could be one of the factors that give it the “endemic and endangered” status.

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