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THE DAMMER BEE, *TRIGONA* AND ITS POLLINATION POTENTIAL IN THE INDIAN FLORA

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ABSTRACT

Trigona is a meliponine bee with wide nesting habits. It is a habitual flower forager and thrives all through the year. An examination of the foraging ecology of this bee with the Indian flora shows that it is polylectic in that it collects pollen and nectar from widely different plant species. It also collects pollen from the nectarless plant species. The floral calender of the bee shows that the plant species bloom at different times of the year and sustain the bee round the year. Flower-opening schedules in the plant species that flower at the same time and occur in the same habitat are separated by time and this situation enables the bee to avoid or overcome competition with other simultaneously foraging insects for the same floral sources. The bee frequents more at white and yellow flowers over other floral colours. It is capable of utilizing floral nectars with widely varying sugar concentrations and located deeply at the flower base. It does not rob floral nectar. _Trigona_ exhibits floral constancy with its pollen collecting behaviour. Besides its leg pollen pellets, it also carries small amount of pollen on its body. Its forage collecting behaviour is reported to effect pollination in most of the plant species it visits. _Trigona_ with wider adaptations to extreme conditions, wider nesting requirements and 'weedy' type of reproduction in warm conditions appears to be superior over _Apis_ bees for consideration as a manageable pollinator.

Key Words: *Trigona*, honey producer, polylectic, foraging behaviour, pollinator, flora, meliponiculture.

INTRODUCTION

In the Indian subcontinent, the Apidae members include social bumblebees, honeybees, and stingless bess (Batra 1977). Of these, the stingless bess occur only in the tropical regions of the world and they are presumed to have originated in South America (Kerr and Maule 1964). They are not truly stingless but the sting is poorly developed. They are also called 'sweat' or dammer bees (Batra 1977; Rajagopal 1998). They exhibit defensive mechanism by biting. The stingless bees belonging to the genus *Trigona* have been widely studied in the tropical world. This genus is much more diversified in the neotropics than in paleotropics; 183 species are known from the neotropics but only 42 have been recognised in Asia (Kerr and Maule 1964).

Trigona iridipennis is the most commonly seen of the three meliponine species in the Indian region, and its nesting habits are relatively well known (Batra 1977). They build nests in the ground, hollows of trees, bamboos, cracks of walls, crevices of culverts, among orchid roots, in empty tanks, boxes, etc. Nest cells are made up of wax and plant resins. A colony consists of a queen, few hundreds to thousands of workers and drones during the breeding season (Rajagopal 1998). Most reproduction occurs from March to June (George 1934).

T. iridipennis and other allied species feed on floral nectar and pollen. They are habitual flower-foragers and occur year-long feeding on various plant species. In particular, *T. iridipennis* is considered to be an important pollinator in certain crops and wild plants rather than a honey producer as it yields very less amount of honey per colony (Rajagopal 1998). To distinguish honey producing *Trigona* from honey bees, they are called honey-making bees.

The stingless bee *T. iridipennis* is most frequently seen in various research papers as a collector of pollen or nectar or both. Although there are other *Trigona* species reported in the Indian region (Batra 1977), the various published works never identified them to species level, but simply mentioned them as *Trigona* sp. or spp. In this paper, the pollination potential of *Trigona* in crops and wild plants is reviewed on the basis of forage plants, their flowering periods, daily flower opening schedules, floral colours, floral forage (pollen and nectar) availability, nectar volume and sugar concentration; and forage type collected, percentage of foraging visits, foraging speed, pollen pick-up efficiency, etc. The name *Trigona* used in this paper refers to *T. iridipennis* unless other-wise specified. This review is expected to form the basis for considering *Trigona* as a potential honey-making bee and pollinator for various crops and wild plants in India.

Floral Calender

Floral calender is a listing of which flowers bloom when and for how long, coupled with their abundance and value to pollinators. Floral calenders can not be applied universally or geographically to the same pollinator species, since the calender of flowering species and their flowering periods vary largely from one place to another. Further, floral calender does not provide blooming sequence of flowers and their development in time. Floral phenology refers to the blooming sequence of flowers and their development in time. Hence, the floral calender and floral phenology are two different concepts and important to pollination and its management.

Trigona lives year-long and utilizes various plant species in its flight range from the nest site. The plant species utilized in the Indian flora have been noted from the published works. They have been listed together with the family, habit and flowering period in Table 1. Fifty nine plant species in thirty six families have been found to be .utilized as pollen and/or nectar source at different times of the year. Further, the plant species represent trees, herbs, shrubs and creepers. Of these, trees and herbs sustain *Trigona* mostly while shrubs and creepers supplement the forage source. A look at the flowering periods shows that the bee is capable of utilizing the floral sources as and when available in order to live year-long. However, the active foraging period appears to be related to the floral sources and density available at any time of the year. Except in dry season, there appears to be plenty of floral forage available from diverse plant species throughout the remaining part of the year. Dry season is the dearth period of floral sources for any flower-dependent animal. The flower-visiting animals should have the skill in handling the flowers of different sizes and varying amounts of pollen and nectar energetically, especially during dearth period. *Trigona* has the skill to utilize certain unrelated flowers of *Tamarindus, Crataeva, Ipomoea, Moringa, Zizyphus, Morinda, Gmelina, Premna, Syzygium, Salvia sp.* (ornamentals), etc. The floral sources come largely from tree species which flower during dry period. Further, the floral source is reliable since trees have the inherent capacity to produce massive flowering on time. Similarly, the tree species such as *Avicennia, Aegiceras, Derris, Ceriops, Combretum,* etc. provide forage for *Trigona* in mangrove habitats. In non-mangrove areas, *Cairica, Evolvulus, Couroupita, Mimosa, Antigonon* flower year-long and nourish *Trigona* bees. These floral sources supplement the main floral calender during dearth period, if available. The floral sources used by *Trigona* indicate that it is polylectic in that it uses flowers

Table 1 *Flowering Seasons of Forage Plants of Trigona*

Family	Plant Species	Habit	Flowering Period	Reference
Alangiaceae	*Alangium salviifolium*	Tree	February - April	Aluri and Reddi 1994b
Anacardiaceae	*Mangifera indica*	Tree	January - March	Chaubal *et al.* 1998
Asteraceae	*Carthamus tinctorius*	Herb	Seasonal crop	Panda *et al.* 1989
	Guizotia abyssinica	Herb	Seasonal crop	Panda *et al.* 1995
	Helianthus annuus	Herb	Seasonal crop	Panda *et al.* 1989
Avicenniaceae	*Avicennia officinalis*	Tree	May - August	Aluri 1990a
Bignoniaceae	*Tecoma stans*	Tree	September - March	Victor 1999
Bombacaceae	*Ceiba pentandra*	Tree	January - March	Lakshmi & Suryanarayana 1997
Brassicaceae	*Brassica nigra*	Herb	Seasonal crop	Panda *et al.* 1989
Caesalpiniaceae	*Bauhinia purpurea*	Tree	October - December	Reddi & Bhaskara Rao 1993
	Peltophorum pterocarpum	Tree	March - June	Aluri and Reddi 1996b
	Tamarindus indica	Tree	April- August	Reddi *et al.* 1997
Capparaceae	*Crataeva magna*	Tree	April- May	Rao *et al.* 1997
Caricaceae	*Carica papaya*	Tree	Year-long	Chaubal *et al.* 1998
Cochlospermaceae	*Cochlospermum religiosum*	Tree	January - April	Reddi *et al.* 1997
Combretaceae	*Terminalia catappa*	Tree	February - March & June - August	Reddi *et al.* 1997
Convolvulaceae	*Evolvulus alsinoides*	Herb	Year -long	Victor 1999
	Ipomoea cairica	Creeper	April- July	Victor 1999
Cucurbitaceae	*Citrullus lanatus*	Herb	Seasonal crop	Mohan Rao & Suryanarayana 1988
	Cucurbita pepo	Herb	Seasonal crop	Chaubal *et al.* 1998
Euphorbiaceae	*Euphorbia tortilis*	shrub	December - March	Reddi *et al.* 1995
	Jatropha gossypiifolia	Herb	June - October	Reddi & Reddi 1983
Fabaceae	*Derris indica*	Tree	March - June	Victor 1999
	Gliricidia sepium	Tree	January - March	Aluri and Reddi 1996a

Family	Plant Species	Habit	Flowering Period	Reference
	Phaseolus vulgaris	Herb	Seasonal crop	Chaubal *et al.* 1998
	Pterocarpus santalinus	Tree	March - May	Rao 1999
	Trigonella corniculata	Herb	Seasonal crop	Mohan Rao 1987
Lamiaceae	*Anisomeles indica*	Herb	November - January	Aluri and Reddi 1989a
	A. malabarica	Herb	October - January	Aluri and Reddi 1989a
	Hyptis suaveolens	Herb	September - November	Aluri and Reddi 1989c; Aluri 1990b
	Leonotis nepetaefolia	Herb	October - January	Aluri and Reddi 1989b; Aluri & Reddi 1994a
	Salvia farinacea	Herb	December - April	Mohan Rao & Singh 1997
	S. *splendens*	Herb	December - April	Mohan Rao & Singh 1997
Lecythidaceae	*Couroupita guianensis*	Tree	Year-long	Aluri and Reddi 1993; Aluri 1993
Liliaceae	*Allium cera*	Herb	Seasonal crop	Mohan Rao and Lazar 1980
Linaceae	*Hugonia mystax*	Shrub	June - September	Aluri *et al.* 1997
Malvaceae	*Hibiscus micranthus*	Shrub	August- December	Victor 1999
Meliaceae	*Azadirachta indica*	Tree	March - May	Aluri 1998
Mimosaceae	*Mimosa pudica*	Herb	Year-long	Aluri, pers. observ.
Moringaceae	*Moringa oleifera*	Tree	February - May & September-November	Jyothi *et al.* 1990
Myrsinaceae	*Aegiceras corniculatus*	Tree	March - May	Aluri 1990a
Myrtaceae	*Syzygium cumini*	Tree	May - June	Victor 1999
Passifloraceae	*Passiflora quadrangularis*	Shrub	Seasonal crop	Chaubal *et al.* 1998
Pedaliaceae	*Pedalium murex*	Herb	July - October	Victor 1999
Polygonaceae	*Antigonon leptopus*	Creeper	Year-long	Kanaka Raju 1999; Aluri *et al.* 1999
Rhamnaceae	*Zizyphus mauritiana*	Tree	September - January & March - June	Rama Devi *et al.* 1989
	Z. oenoplia	Shrub	August - December & March - June	Atluri *et al.* 1995
Rubiaceae	*Morinda tomentosa*	Tree	April- August	Victor 1999
Rutaceae	*Citrus reticulata*	Tree	February - October	Kumar & Lenin 1998

Family	Plant Species	Habit	Flowering Period	Reference
Sapindaceae	*Allophylus serratus*	Shrub	August - September	Aluri *et al.* 1998
	Cardiospermum halicacabum	Creeper	June - December	Ramadas *et al.* 1997
	Litchi chinensis	Tree	Seasonal crop	Chaubal *et al.* 1998
	Sapindus emarginatus	Tree	November - January	Reddi *et al.* 1983
Sterculiaceae	*Helicteres isora*	Tree	July - October	Atluri *et al.* 2000
	Sterculia foetida	Tree	January - March	Rao 1999
Verbenaceae	*Gmelina asiatica*	Shrub	February - October	Reddi *et al.* 1996
	Premna latifolia	Tree	March - November	Aluri, unpublished
	Tectona grandis	Tree	June - November	Reddi *et al.* 1997
Zingiberaceae	*Elettaria cardamomum*	Herb	Seasonal crop	Chaubal *et al.* 1998

belonging to diverse genera and families. As already mentioned, the floral calender of *Trigona* must be prepared for each region based on the general floral calender presented in Table 1. Although *Trigona* is able to exploit forage from different plant species in the same season, its preferred floral calender may be different. Nevertheless, the floral calender is a must for sustaining *Trigona* year-long.

In agro-habitats, vegetable and fruit crops provide ample pollen and nectar during the entire flowering season. Additionally, the wild vegetation consisting of various plant species may supplement the main food source and may also nourish *Trigona* when crops are not in bloom. Here, the floral calender would be different. Further, the degradation of the wild vegetation may exhibit a profound influence on the occurrence and survival of *Trigona* in agro-habitats. Because, the decline or loss of wild vegetation may eliminate nesting sites and forage plants of *Trigona.* The wild vegetation sustains *Trigona,* especially when crops are not in bloom. Since the bee is a short-distance flier from its nesting site, the forage from wild plant/crops must be available within its distance range, or else *Trigona* populations either decline or disappear in the area depending on the forage availability.

Flower-opening Schedules

Daily flower-opening schedules are available for 46 plant species out of total 59 plant species foraged by *Trigona* (Table 2). These schedules show that 14 plant species anthese before sunrise between 0200-0600 h, 17 between sunrise and noon, 5 from morning to evening, 9 from evening to midnight, and 1 round the clock. Temporal separation of anthesis schedules from dawn to dusk in plant species which bloom at the same time and occur in the same habitat enables *Trigona* to shift from one plant species to another according to its food requirement within its flight distance range from the nesting site. Since the bee is polylectic in character, it is no wonder to find mixed pollen types in its pollen loads. Further, the bee usually begins its foraging activity after sunrise by which time other insects that begin foraging activity before sunrise, specially honeybees may deplete floral forage to some extent. Therefore, *Trigona* would have to shift to other appropriate flower types available in the habitat for collecting floral forage. Nevertheless, anthesis schedules of different plant species flowering in the same season and occurring in the same habitat play an important role in directing *Trigona* to locate rewarding flower types through the day from dawn to dusk. Further, such a situation enables the bee to avoid or overcome competition with other bees/insects for the same floral food sources.

Table 2 Floral Details of Forage Plants of ***Trigona***

Family	Plant species	Anthesis Time (h)	Flower colour	Forage collected Pollen/Nectar	Forager/ Pollinator	Pollen output/flower	Nectar volume (μl)	Nectar sugar conc. (%)	Reference
Alangiaceae	*Alangium salviifolium*	24 - hrs.	Dirty white	Pollen + Nectar	Pollinator	27,300	n/a	25-29	Aluri & Reddi 1994b Reddy & Aruna 1990
Anacardiaceae	*Mangifera indica*	n/a	Cream	Nectar	Pollinator	n/a	n/a	n/a	Chaubal *et al.* 1998
Asteraceae	*Carthamus tinctorius*	n/a	Yellow	Pollen + Nectar	Pollinator	n/a	n/a	n/a	Panda *et al.* 1989
	Guizotia abyssinica	n/a	n/a	Pollen + Nectar	Pollinator	n/a	n/a	29	Panda *et al.* 1995 & Zmarlicki 1980
	Helianthus annuus	0600-0800	Yellow	Pollen + Nectar	Pollinator	n/a	n/a	n/a	Panda *et al.* 1989
Avicenniaceae	*Avicennia officinalis*	0500-1900	Yellow	Pollen	Pollinator	13,480	Traces	n/a	Aluri 1990a
Bignoniaceae	*Tecoma stans*	0500-0700 &1500-1700	Yellow	Pollen + Nectar	Pollinator	n/a	n/a	n/a	Victor 1999
Bombacaceae	*Ceiba pentandra*	1900	Dusty white	Pollen + Nectar	Pollinator	42,000	160	12-19	Lakshmi & Suryanarayana 1997
Brassicaceae	*Brassica nigra*	n/a	Yellow	Pollen + Nectar	Pollinator	n/a	n/a	49	Panda *et al.* 1989 & Sharma 1958
Caesalpiniaceae	*Bauhinia purpurea*	0430-0500	Purple	Pollen	Pollinator	66,000	Traces	5-7	Reddi & Bhaskara Rao 1993
	Peltophorum pterocarpum	0600-1500	Yellow	Pollen + Nectar	Pollinator	n/a	Traces	n/a	Aluri and Reddi 1996b
	Tamarindus indica	2300-0400	Dusty white	Nectar	Forager	18,600	1	6-8	Reddi *et al.* 1997
Capparaceae	*Crataeva magna*	1730-1830	White	Pollen + Nectar	Forager	2,95,000	n/a	n/a	Rao *et al.* 1997
Caricaceae	*Carica papaya*	n/a	Cream	Nectar	Pollinator	n/a	n/a	n/a	Chaubal *et al.* 1998
Cochlospermaceae	*Cochlospermum religiosum*	2300-2400	Yellow	Pollen	Forager	2,11,09,000	No secretion	-	Reddi *et al.* 1997
Combretaceae	*Terminalia catappa*	0300-0500	Cream	Pollen	Pollinator	19,250	Traces	n/a	Reddi *et al.* 1997
Convolvulaceae	*Evolvulus alsinoides*	0600-0700	White	Pollen + Nectar	Pollinator	n/a	n/a	n/a	Victor 1999
	Ipomoea cairica	1000-1100	Pink	Pollen + Nectar	Pollinator	n/a	n/a	n/a	Victor 1999
Cucurbitaceae	*Citrullus lanatus*	0600-0700	Yellow	Pollen + Nectar.	Forager	n/a	n/a	n/a	Mohan Rao & Suryanarayana 1988
	Cucurbita pepo	n/a	Yellow	Nectar	Pollinator	n/a	n/a	n/a	Chaubal *et al.* 1998
Euphorbiaceae	*Euphorbia tortilis'*	0730-1000	Yellow	Pollen + Nectar	Pollinator	765	Traces	n/a	Reddi *et al.* 1995
	Jatropha gossypiifolia	0600-0700	Purplish-red	Nectar	Pollinator	880	n/a	n/a	Reddi & Reddi 1983
Fabaceae	*Derris indica*	0900-1100	Violet	Pollen	Pollinator	n/a	n/a	n/a	Victor 1999
	Gliricidia sepium	0730-1600	Lavender	Pollen + Nectar	Pollinator	n/a	3-4	34	Aluri and Reddi 1996a
	Phaseolus vulgaris	n/a	White	Nectar	Pollinator	n/a	n/a	n/a	Chaubal *et al.* 1998
	Pterocarpus santalinus	2330-0030	Yellow	Pollen	Pollinator	34,800	Traces	n/a	Rao 1999
	Trigonella corniculata	1100-1800	Yellow	Pollen + Nectar	Forager	n/a	n/a	n/a	Mohan Rao 1987
Lamiaceae	*Anisomeles indica*	0530-0730	Purple	Pollen	Pollinator	7,440	1.6	32-43	Aluri & Reddi 1989a
	A. malabarica	0100-0500	Purple	Pollen	Pollinator	9,424	1.8	30-48	Aluri & Reddi 1989a
	Hyptis suaveolens	0700-1700	Violet	Pollen	Pollinator	2,520	0.9	6-8	Aluri & Reddi 1989c
	Leonotis nepetaefolia	2200-0200	Scarlet	Pollen	Pollinator	10,412	6	18	Aluri & Reddi 1989b
	Salvia farinacea	n/a	White	Nectar	Forager	n/a	n/a	n/a	Mohan Rao & Singh 1997
	S. splendens	n/a	Red	Nectar	Forager	n/a	n/a	n/a	Mohan Rao & Singh 1997

Family	Plant species	Anthesis Time (h)	Flower colour	Forage collected Pollen/Nectar	Forager/ Pollinator	Pollen output/flower	Nectar volume (µl)	Nectar sugar conc. (%)	Reference
Lecythidaceae	*Couroupita guianensis*	0700	Rosy-yellow	Pollen	Pollinator	Abundant	No secretion	n/a	Aluri and Reddi 1993; Aluri 1993
Liliaceae	*Allium cepa*	n/a	White	Pollen + Nectar	Pollinator	n/a	n/a	59-75	Mohan Rao and Lazar 1980
Linaceae	*Hugonia mystax*	0500-0800	Yellow	Pollen + Nectar	Pollinator	18,850	Traces	n/a	Aluri *et al.* 1997
Malvaceae	*Hibiscus micranthus*	0630-0800	Pink & white	Pollen + Nectar	Forager	n/a	n/a	n/a	Victor 1999
Meliaceae	*Azadirachta indica*	0200-1000	White	Pollen	Pollinator	n/a	Traces	n/a	Aluri 1998
Mimosaceae	*Mimosa pudica*	0400-0500	Rose	Pollen	Pollinator	17,320	n/a	n/a	Aluri, pers. observ.
Moringaceae	*Moringa oleifera*	0500-0900	White	Nectar	Pollinator	2,46,000	1.3	5-18 40	Jyothi *et al.* 1990 & Bhat *et al.* 1987
Myrsinaceae	*Aegireras corniculatus*	0500-1000	White	Pollen	Pollinator	9,530	No secretion	n/a	Aluri 1990a
Myrtaceae	*Syzygium cumini*	0900-1100	White	Pollen + Nectar	Pollinator	n/a	9-72	n/a	Victor 1999 & Satyanarayana 1975
Passifloraceae	*Passiflora quadrangularis*	n/a	n/a	Nectar	Pollinator	n/a	n/a	n/a	Olaubal *et al.* 1998
Pedaliaceae	*Pedalium murex*	0600-0700	Yellow	Pollen + Nectar	Pollinator	n/a	n/a	n/a	Victor 1999
Polygonaceae	*Antigonon leptopus*	0600-0800	Pink & white	Pollen + Nectar	Pollinator	1,480	1.5	26-28	Kanaka Raju 1999 Aluri *et al.* 1999
Rhamnaceae	*Zizyphus mauritiana*	0600-1000	White	Pollen + Nectar	Pollinator	4,900	2.5	30 40	Rama Devi *et al.* 1989 & Zmarlicki 1980
	Z. oenoplia	0930-1030	White	Pollen + Nectar	Pollinator	4,975	Traces	15	Aluri *et al.* 1995
Rubiaceae	*Morinda tomentosa*	1700-1900	White	Pollen	Pollinator	n/a	n/a	n/a	Victor 1999
Rutaceae	*Citrus reticulata*	0500-0700	White	Pollen + Nectar	Pollinator	n/a	n/a	n/a	Kumar & Lenin 1998
Sapindaceae	*Allophylus serratus*	0200-0500	White	Pollen + Nectar	Pollinator	4,432	Traces	n/a	Aluri *et al.* 1998
	Cardiospermum halicacabum	0500-0900	White	Pollen + Nectar	Pollinator	2,880	Traces	n/a	Rama Das *et al.* 1997
	Litchi chinensis	n/a	n/a	Nectar	Pollinator	n/a	n/a	61-78	Chaubal *et al.* 1998 & Nair 1983
	Sapindus emarginatus	0520-0700	Cream	Nectar	Pollinator	57,775	St-4 Pst-11	22-48	Reddi *et al.* 1983
Sterculiaceae	*Helicteres isora*	0300-0330	Greyish-blue	Pollen + Nectar	Forager	97,700	205	10-16	Aluri *et al.* 2000
	Sterculia foetida	0700-1000	Red	Pollen + Nectar	Forager	37,500	Traces	n/a	Rao 1999
Verbenaceae	*Gmelina asiatica*	0500-0600	Yellow	Pollen	Forager	47,120	75-80	20-28	Reddi *et al.* 1996
	Premna latifolia	0700-1200	White	Pollen + Nectar	Pollinator	n/a	n/a	n/a	Aluri, unpublished
	Tectona grandis	0300-0400	White	Pollen + Nectar	Pollinator	12,650	Traces	n/a	Reddi *et al.* 1997
Zingiberaceae	*Elettaria cardamomum*	n/a	n/a	Nectar	Pollinator	n/a	n/a	n/a	Chaubal *et al.* 1998

St : Staminate flowers
Pst: Pistillate flowers
n/a : data not available

Floral Colouration

Kevan (1983) made an exhaustive review of floral colour recognition and preferences by insects. He states that insects adapt to photic environment and distinguish colours. They exhibit trichromatic color vision. The colours we see are not the same for them. What we call yellow is "insect-red", blue is "insect-green" and ultraviolet is "insect-blue". White reflects all wavelengths in equal proportions in a spectrum of natural light within the range of sensitivity of that given colour sensor or primary colours of that colour sensor. In effect, insects have the ability to recognise a colour from the white surface.

Kevan in his review based on his own work and also on others work suggests that insects visit yellow and white flowers very widely. Very often, these flowers reflect ultraviolet radiation, although it does not impart special attractiveness to the flowers. Among insects, bees frequent blue or purple flowers and blue is their favourite colour. Some bees visit red flowers which reflect ultraviolet.

From the foregoing, it is obvious that colour is an important floral attribute. It functions as a long distance signal, especially, to actively flying diurnal insects. The array of floral colours visible to insects allows them to distinguish species of flowers at a distance. From Table 2, it is obvious that *Trigona* has the ability to recognise floral colours and frequent more at white and yellow-flowered species. This bee also visits flowers of other colours such as purple-pink, red, violet, lavender, scarlet and greyish blue. It appears that these floral colours reflect in ultraviolet which the bee is able to recognize it as "insect-blue". However, the dominance of yellow and white-flowered species and only one blue-flowered species in the list of forage plants of *Trigona* indicates that blue is not a favourite colour for the bee and disagrees with the generalization that blue is the most favourite colour for bees, *sensu* Kevan (1983). Whatever be the floral colour, it must reflect the colour that the bee is able to identify in order to be visited by it.

Floral Rewards

Floral colour is the main visual attractant for the insects. Other visual attractants that aid insects include floral shape, size and guides. The floral guides may be olfactory, structural, or visual and operate in short range orientation of insects. All these attractants together aid in the recognition and discrimination of flowers in order to obtain food from the rewarding flowers (Kevan 1983; Dafni and Kevan 1996). The references from which the list of forage plants of *Trigona* is prepared do not give any information with regard to the visual attractants other than floral colour in the recognition and discrimination of flowers. Therefore, it is not possible to examine their role in drawing the attention of *Trigona* to the flowers. However, there is some information on the flower size and shape. It shows that *Trigona* forages the flowers of various sizes and shapes. It means that the bee does not appear to discriminate flowers exclusively on the basis of visual attractants but largely on the accessibility of food in the flowers. Further, the bee does not make any attempt to rob floral rewards, if inaccessible. It simply avoids foraging on such flowers. A study made by Barrows (1976) in the neotropics shows that *Trigona fulviventris* robs the nectar of *Lantana camara* by making holes in the corolla base of the flowers. Although L. *camara* is the most commonly occurring species in India, *Trigona* is never reported to visit its flowers and also its robbing behaviour is ruled out in all the plant species reported to be foraged by it.

The floral rewards include both nectar and pollen. The nectar volume and its sugar concentration, and also pollen output per flower for some plant species foraged by *Trigona* are available (Table 2). The data show that the bee is capable of collecting nectar secreted even in trace amount in the flowers of some plant species. The nectar volume ranges from 0.9 to 205 µl per flower. The sugar concentration in the nectar varies from 5 to 75% which shows that the bee utilizes both dilute as well as highly concentrated sugars in the floral nectar. This versatality enables it to sustain even when its preferred range of sugar concentrations becomes unavailable. Pollen output/flower ranges between 765 and 2,11,09,000; these values are two extremes. The pollen is abundant in most of the plant species at flower and plant level at any given time during flowering period.

Of the total plant species foraged by the bee, 3 are nectarless and all others nectariferous. The nectarless plant species offer only pollen as floral reward. Among the nectariferous plant species, the bee collects only nectar from *Mangifera, Carica, Cucurbita, Jatropha, Phaseolus, Moringa, Passiflora, Litchi, Sapindus, Elettaria, Tamarindus* and *Salvia;* and it collects only pollen from *Avicennia, Bauhinia, Pterocarpus, Anisomeles, Hyptis, Leonotis, Gmelina, Terminalia, Derris, Azadirachta* and *Mimosa.* It collects both pollen and nectar in the same or different foraging visits from all other nectariferous plant species. It appears that the bee, although polylectic in forage collection from diverse plant species, is selective in collecting pollen and/ or nectar from its forage plants, even if it has access to the floral rewards.

Foraging Behaviour Versus Pollination

The bee usually collects floral rewards in "mess and soil" manner from both nectariferous and nectarless flowers. It approaches the flowers always in upright position and settles on petals or stamens. Once it settles on the flower, it gradually moves towards the anthers or the flower base for collecting floral reward. To gather pollen, it simply shakes the anthers. It lacks the ability to discriminate the stigma from the anthers. If the stigma and anthers are intermingled, stand at the same level and attain maturity at the same time, the pollen collecting behaviour of the bee results in pollination. To collect nectar, usually but not always, the bee finds its way into the flower base bypassing the pollination apparatus. It is surprising to note that in *Tecoma stans,* the bee enters the long tube of the flower, collects nectar, and comes out by moving backwards. It never attempts to rob the nectar by biting holes at the base of the corolla tube. This nectar collecting behaviour enables the bee to get floral reward but it results in depleting nectar source for the appropriate pollinator. In majority of the plants that the bee visits, it is the pollen collecting behaviour which largely accounts for pollination.

Table 2 shows that the bee does not act as pollinator in all the plant species it visits. It acts as mere forager without effecting pollination in *Tamarindus, Crataeva, Cochlospermum, Citrullus, Trigonella, Salvia, Hibiscus, Helicteres, Sterculia* and *Gmelina.* In all other plant species, the bee is implicated to have a role in pollination. Its role as "minor" or "major" pollinator depends on the presence or absence of other foraging insects. No report has mentioned that the bee has the potential of robbing the flowers or defend them from the legitimate pollinators. It simply gathers the floral rewards silently and gets disturbed in the presence of medium to large bodied insect species. Sometimes, it even keeps away from the flowers when other bees come to forage. On the contrary, Macfarlane (1995) reports that *Trigona* in South America has the potential for robbing flowers of nectar and pollen, while aggressively defending them from legitimate or appropriate pollinators.

Foraging Activity

None of the plant species listed in Table 1 and 2 is exclusively foraged by *Trigona.* Along with this, other bees and also other insects comprising of wasps, butterflies, flies, thrips, ants and birds and bats forage for the floral rewards. The total percentage of foraging visits of *Trigona* relative to other foraging insects is an important parameter to evaluate its floral constancy and role in depletion of floral rewards as forager or in effecting pollination. The data on the percentage of foraging visits of *Trigona* relative to other insects are available only for 19 plant species and the same are presented in Table 3. The data show that *Trigona* is the principal pollinator of *Jatropha, Allium, Citrus, Hugonia, Zizyphus mauritiana* and *Sapindus.* This bee contributes to the tune of 0.5 to 19% of the total foraging visits on other plant species and if these percentages are compared with the foraging visits of individual species of other insects, the foraging visits (%) of *Trigona* are prominent and contribute to effective removal of floral rewards.

Table 3 Foraging Visits (%) of *Trigona* Relative to Other Foragers on Different Plant Species

Family	Plant species	Foraging visits						Reference
		Trigona	Other Bees	Wasps	Butter-flies	Flies	Birds	
Caesalpiniaceae	*Bauhinia purpurea*	5	92	1	2	-	-	Reddi & Bhaskara Rao 1993
Euphorbiaceae	*Euphorbia tortilis*	9	54	19	-	18	-	Reddi *et al.* 1995
	Jatropha gossypiifolia	57	19	8	8	8	-	Reddi & Reddi 1983
Fabaceae	*Pterocarpus santalinus*	10	79	-	11	-	-	Rao 1999
Lamiaceae	*Anisomeles indica*	19	67	-	3	-	11	Aluri & Reddi 1989a
	A. malabarica	0.5	93	0.5	2	-	4	Aluri & Reddi 1989a
	Hyptis suaveolens	4	79	-	17	-	-	Aluri & Reddi 1989c
Liliaceae	*Allium cepa*	47	53	-	-	-	-	Mohan Rao & Lazar 1980
Linaceae	*Hugonia mystax*	37	60	-	3	-	-	Aluri *et al.* 1997
Moringaceae	*Moringa oleifera*	8	86	-	6	-	-	Jyothi *et al.* 1990
Polygonaceae	*Antigonon leptopus*	7	84	2	2	5	-	Kanaka Raju 1999
Rhamnaceae	*Zizyphus mauritiana*	31	45	16	-	8	-	Rama Devi *et al.* 1989
Rutaceae	*Citrus reticulata*	41	36	-	23	-	-	Kumar & Lenin 1998
Sapindaceae	*Allophylus serratus*	11	48	38	3	-	-	Aluri *et al.* 1998
	Cardiospermum halicacabum	13	71	13	1	2	-	Ramadas *et al.* 1997
	Sapindus emarginatus	27	63	8	1	1	-	Reddi *et al.* 1983
Sterculiaceae	*Helicteres isora*	11	51	6	9	-	23	Atluri *et al.* 2000
Verbenaceae	*Gmelina asiatica*	9	91	-	-	-	-	Reddi *et al.* 1996
	Tectona grandis	8	14	20	38	20	-	Reddi *et al.* 1997

- : no visits

Infact, all the plant species listed in Table 3 except *Helicteres* and *Gmelina* are pollinated by *Trigona*. With this bee populations alone or alongwith other insects, pollination may be effected in these plant species. *Helicteres* and *Gmelina* do not get benefitted by the visits of the bee. The bee uses *Helicteres* as pollen and nectar source and *Gmelina* as pollen source only though the latter also produces ample amount of nectar.

Foraging Speed and Pollen-Pick Efficiency

The data regarding foraging time per flower, number of flowers foraged/ minute and pollen found on the body of the bee are available for a few species only (Table 4). The bee is a slow mover and also a slow collector of floral rewards. In effect, it cannot forage too many flowers in a short span of time. Such a tendency of the bee largely accounts for autogamous or geitonogamous pollinations. Since no plant species is exclusively foraged by it, the depletion of floral rewards by other simultaneously foraging insects compels the bee to make inter-plant movements in quest of floral food and in consequence, cross-pollination is also effected by the bee. Body washings of the bee for pollen show that it carries small amounts of pollen but it is sufficient to pollinate flowers. In addition, the bee loads its corbiculae with pollen and can be seen even with the naked eye. The bee with pollen loads coupled with its mess and soil manner of pollination and intra/inter-plant movements bring about self- and cross-pollination without fail. The bee with all these characters makes up a reliable pollinator.

DISCUSSION

Savoor (1998) laments that research activity in India on bees is in a state of neglect and recourse to pollinator management aimed at enhanced crop production is practically unknown. It is true that much attention has not been devoted to this field. Savoor (1998) also states that additional yields could be obtained with bee pollination in various crops. For enhancing productivity, especially of oil seeds, bee pollination is unavoidable. The crops such as mustard, gingely, niger and safflower do not give potential yields unless bees are provided during the flowering period. Similar situation holds true for the majority of wild plant species in India. Viewed from this perspective, bees have a vital role in the pollination of crops and wild plants. Enhanced yields in crops and seed production in wild plants associated with bee pollination are bound to better the country's economy. Further, the country would also save larger amounts by minimising the import of edible oils.

Since bee-pollination has a tremendous role in fruit or seed production, be it crops or wild plants, the bee species which can be managed easily are of great value for enhanced yields in crops and also for the perpetuation and conservation of various wild plant species in forests and also in anthropogenic habitats. Honey bees have been in use for long to get enhanced yields in some crops. No effort has been made to find new bee species from time to time for enhanced yields in various crops in India which is primarily agriculture-oriented. On the contrary, the U.S. Department of Agriculture with the Bee Biology and Systematics Laboratory, Logan, Utah has identified several new bee species and developed them to commercially managed pollinators of various crops. Viewed from this angle, India with its vast bee diversity has wide scope for identifying the wild bee species which are of great value as commercially manageable pollinators.

Trigona is polylectic and collects both pollen and nectar round the year. It mostly utilizes nectariferous flowers because they offer both pollen and nectar and obtainable in the same foraging visit with less energy expenditure. The bee is relatively more efficient in pollination compared to honeybees and has the ability to occupy different nest sites as unmanaged pollinators, *sensu* Macfarlane (1995). The bee is shown to interfere with the activity of honeybees by attacking them at the flowers (Macfarlane 1995). With the known information on the foraging behaviour of *Trigona* in the Indian flora, it is found that the bee does not interfere with honeybees and collect floral rewards in perfect harmony with honeybees at the same time. Koeniger (1995) carried out an experiment and observed similar coexistence and interaction of *Trigona iridipennis* with other honeybees. He trained the honeybees and *Trigona* to feed at a common feeding dish simultaneously. *Trigona* was found to forage on many plant species with its small flight range and it showed a higher tendency to defend the feeding dish. Roubik (1995) states that *Trigona* is the effective pollinator of coconuts despite its interference with honeybees at the flowers; effective pollinator for within-plant crossing in *Solanum* species; and effective pollinator for outcrossing in *Carica papaya, Citrullus lanatus, Manihot esculenta,* etc. in tropical America. It suggests that *Trigona* is an effective pollinator enforcing both self and cross pollination and its potential as a pollinator against honeybees assumes significance.

The *non-Apis* bees in general have higher degree of specialization or adaptation to more extreme conditions that make them valuable. *Trigona* is one such bee which is adapted to wide variations in abiotic and biotic environment. Meliponiculture in which *Trigona* is a member is widely practised in tropical america. Wild colonies of stingless bees can be transferred to wooden hives and managed under human care. Indeed, they have been domesticated and used for crop pollination and for honey source. Suitable stingless bees, in addition to *Trigona* can be exploited for effective pollination in crops since their nesting sites vary

Table 4 Foraging Time and Pollen Pick-up by *Trigona* on Different Plant Species

Family	Plant species	Foraging time/flower (sec.)	Flowers foraged (min.)	Pollen found in body washings	Reference
Avicenniaceae	*Avicennia officinalis*	22	4	n/a	Reddi *et al.* 1995
Caesalpiniaceae	*Bauhinia purpurea*	21	3	39	Reddi & Bhaskara Rao 1993
Euphorbiaceae	*Euphorbia tortilis*	9	7	63	Reddi *et al.* 1995
	Jatropha gossypiifolia	6	8	20	Reddi & Reddi 1983
Fabaceae	*Pterocarpus santalinus*	10	7	85	Rao 1999
Lamiaceae	*Anisomeles indica*	5	22	n/a	Aluri & Reddi 1989a
	A. *malabarica*	8	10	n/a	Aluri & Reddi 1989a
	Hyptis suaveolens	4	17	70	Aluri & Reddi 1989c
	Leonotis nepetaefolia	7	10	n/a	Aluri & Reddi 1994a
Liliaceae	*Allium cepa*	n/a	3	n/a	Mohan Rao & Lazar 1980
Linaceae	*Hugonia mystax*	19	2	n/a	Aluri *et al.* 1997
Moringaceae	*Moringa oleifera*	4	6	n/a	Jyothi *et al.* 1990
Rhamnaceae	*Zizyphus mauritiana*	4	11	581	Rama Devi *et al.* 1989
	Z. *oenoplia*	4	7	430	Atluri *et al.* 1995
Sapindaceae	*Allophylus serratus*	7	9	n/a	Aluri *et al.* 1998
	Cardiospermum halicacabum	12	2	n/a	Ramadas *et al.* 1997
	Sapindus emarginatus	12	4	60	Reddi *et al.* 1983
Sterculiaceae	*Helicteres isora*	11	5	4212	Atluri *et al.* 2000
Verbenaceae	*Gmelina asiatica*	8	6	n/a	Reddi *et al.* 1996

n/a : data not available

greatly and usually available in nature. Hives for *Trigona* bees may be designed with wooden material suitably to accommodate their colonies and for easy access by the beekeeper. Each colony produces upto 1 litre of honey and the honey is assigned to have great medicinal properties and sold at a high price to local pharmacies in Costa Rica (Roubik 1995). To nourish *Trigona* bees round the year, hedges, field boundaries, home gardens, etc. may be developed in agricultural and anthropogenic habitats. A few stingless bees including *Trigona* bees are highly adapted to disturbed habitats such as cities or areas with little forest. The warm climate in these areas permit more reproduction and in effect, may become 'weedy' in the sense that they propagate rapidly when able to find nesting sites often provided by holes in cement block, stone buildings or walls, structural timber with hollow sections or in bamboo internodes. Their propagation in huge numbers in urban areas may be profitably used for *Trigona-keeping* for honey. The avenue tree species grown in cities if included with economically important ones would provide food for *Trigona* and also for better yields by quality and quantity. In India, *Trigona* bees should be given a top priority against honeybees in order to initiate diversification of bee species in bee-keeping and also to get higher returns from crops and economically important wild plants through pollination. The known forage plant species of *Trigona* are small when compared to the size of plant diversity in India. Further, the known information on the foraging behaviour of *Trigona* in the native flora is highly incomplete to draw any solid inference. Therefore, the data included in the paper should be used as basis for further studies in a holistic approach in order to exploit the potential of *Trigona* for pollination and honey-making, and better agricultural economy.

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