

Nesting habits, floral resources and foraging ecology of large carpenter bees (*Xylocopa latipes* and *Xylocopa pubescens*) in India

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Information on nesting, floral resources, floral characteristics and foraging ecology of two large carpenter bee species, *Xylocopa latipes* and *X. pubescens* in India has been reviewed. The review suggests that *Xylocopa* bees in general and *X. latipes* and *X. pubescens* in particular utilize almost the same wood materials for nesting and floral resources for food. The bees are characteristically multivoltine, provided there are adequate floral resources throughout the year in a habitat. They are bivoltine in habitat, where there are inadequate floral resources. Female bees collect pollen and nectar for production of offspring and floral reward for their own maintenance; male bees collect only nectar. However, the bees utilize a limited number of plant species, a few of which produce only pollen and all others both pollen and nectar.

Keywords: Conservation and management, floral resources, foraging ecology, nesting habits, *Xylocopa*.

CARPENTER bees with 400 species (family Anthophoridae; order Hymenoptera)¹ resolved into large (genus *Xylocopa*) and small (genus *Ceratina*), are cosmopolitan but mainly pantropical, and are characterized by making tunnels for nesting in solid wood or in stumps, logs or dead branches of trees². The Indian bee fauna has a prominent component of carpenter bees occurring throughout the year and foraging on a wide array of flowers during the day or sometimes even during moonlit nights. The present article relates to two species of *Xylocopa* (*X. latipes* Drury and *X. pubescens* Spinola), with particular reference to their nesting and foraging behaviour.

Nesting habits

Dead wood, pithy stems and bamboo culms are commonly used for nesting associated with plants like *Syzygium cumini* and *Cassia siamea*³. Females of both the insect species are involved in nest construction, digging tunnels or holes in the selected wood with their strong and well-developed mandibles, taking about one week time. This is

followed by gathering of pollen mixed with nectar from different flower types available in the habitat for transfer to brood chambers in the nesting hosts, with slight changes in brooding pattern varying from two to four generations per year spread over February–November or even restricted to March–April and August–September, suggesting a complementarity between forage and nesting^{3–6}. While it takes two months for the juvenile broods to emerge, the same nest is reused over and over again, unless it is disturbed by fuel-wood gatherers, enforcing new efforts for nesting.

Floral resources

The relationship between bees and flowers is mutualistic, the former for food and the latter for pollination which is a key aspect in the sexual reproduction of plants, enabled by appropriate structural and functional characteristics. Pollen plant resources reported include *Cochlospermum religiosum*, *Cassia*, *Solanum* species and *Peltophorum pterocarpum*^{3,7,8}.

It is of special interest to note that nectar and pollen are required from the same source in rare instances. Further, the procurement of oil-rich pollen from plants belonging to Cucurbitaceae, Melastomataceae, Solanaceae, Primulaceae and Gesneriaceae and species like *P. pterocarpum*^{3,8}, using lipid secretions in place of nectar or oil for waterproof cell linings in the nest, and such behavioural phenomenon deserve new research attention. Floral rewards, pollen and nectar to be precise, form the criterion for forage behaviour, being either oligolectic or polylectic, involving travelling of the bees even long distances for gathering food resources (Figures 1 and 2).

Both female and male bees of these two species collect nectar from several plant species belonging to different families (polylecty). The nectar plants reported include *Alangium salviifolium*, *Calotropis gigantea*, *C. procera*, *Tecoma stans*, *Bauhinia purpurea*, *B. racemosa*, *B. variegata*, *Crotalaria laburnifolia*, *C. verrucosa*, *Gliricidium sepium*, *Pongamia pinnata*, *Tephrosia purpurea*, *Anisomeles indica*, *A. malabarica*, *Careya arborea*, *Moringa oleifera*, *Antigonon leptopus*, *Gmelina arborea*, *G. asiatica* and *Tribulus terrestris* (Table 1).

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Floral characteristics

In accordance with functional requirements of procurement of pollen and nectar by the carpenter bees, the flower characters are designed and constructed in such a way that the flowers are able to hold the bees and also withstand the labourious rough footwork of the bee visitor to the flowers, in extracting the food materials⁹. Among the characters of such flowers, corolla with strong walls and other protecting devices that prevent nectar-robbing, anthers specialized for pollen collection by bees, with sexual organs touching the dorsal or ventral side depending on features such as placement of stamens in the flower, having pale or saturated colours, with a fresh odour and ephemeral day-blooming and sparse nectar production may be mentioned. Such characteristics occur typically in *A. salviifolium*, *Calotropis* species, *Bauhinia* species, *Cassia* species, *P. pterocarpum*, *Cochlospermum religiosum*, *Crotalaria* species, *G. sepium*, *P. pinnata*, *T. purpurea*, *Anisomeles* species, *M. oleifera*, *Solanum* species and *Gmelina* species. Among these, *Cassia* species receive visits exclusively from *Xylocopa* bees³, while all others from other bees and insects also^{6,10–14}. Further, birds have also been reported to visit *A. salviifolium*, *Calotropis* species, *Anisomeles* species and *M. oleifera*, although these flowers are not functionally quite appropriate for them^{6,11,13,15}. *Xylocopa* bees collect pollen legitimately from nectarless flowers and nectar legitimately from all nectariferous

plant species, except *Tecoma stans* in which the flowers are punctured at the base of the corolla to reach the nectar source deeply hidden in the narrow part of the corolla tube. Other plant species such as *C. arborea*, *A. leptopus* and *T. terrestris* are similarly favoured when preferred flowers are not available^{16–18}.

Features of the flower, such as colour, odour, size and shape associated also by symmetry, anthesis, nectar production, among other minor attributes play a part in the success of forage collection by the bees.

Colour

Having a trichromatic colour vision, insects in general have the ability to recognize and distinguish colours. It has been noted¹⁹ that insects visit yellow and white flowers widely, but bees frequently visit blue or purple flowers with blue as the most favourite colour, some even visiting red flowers, which reflect ultraviolet light. *Xylocopa* bees prefer mostly yellow followed by purplish-white, creamy white and bluish white (Table 1) flowers.

Odour

Floral odours are diverse and have evolved to attract potential pollinators. Animal-pollinated flowers produce pleasant or foetid odours and nectar for attracting and distinguishing pollinators. *Xylocopa* flowers (Table 1) show that most of the nectar-producing plant species are odouriferous and the bees may use this odour which varies with plant species as a cue to visit the right flowers, as against odourless pollen plants which are supplemented with yellow anthers and pollen. *P. pterocarpum* is an exception in that it produces odourless, nectariferous flowers, but the attraction here seems to be the yellow flowers, anthers and pollen²⁰.

Size

Flower size has a special functional significance in plant–forager association, and evolutionary shift from outcrossing to selfing is mediated through decreased flower size and alterations in floral morphology²¹. *Xylocopa* bees prefer flowers which are usually medium-sized, but also use large flowers if available, accessible and rewarding by exhibiting flower fidelity²². Plants like *A. leptopus* and *T. terrestris* with small flowers are not appropriate for visitation by *Xylocopa* bees, but the latter still use them as nectar source opportunistically.

Shape and symmetry

Shape coupled with pattern (symmetry) plays an important role for *Xylocopa* bees to make visits and subsequently



Figure 1. Nectar flowers of *Xylocopa* bees: **a**, *X. latipes* on *Crotalaria laburnifolia*; **b**, *X. latipes* on *Crotalaria verrucosa*; **c**, *X. pubescens* on *C. verrucosa*; **d**, *X. pubescens* on *Peltophorum pterocarpum*.



Figure 2. Pollen and nectar flowers of *Xylocopa* bees. **a–c**, Pollen flowers: **a**, *X. pubescens* on *Cassia alata*; **b**, *X. latipes* on *Cassia siamea*; **c**, *X. latipes* on *Cassia auriculata*. **d, e**, Nectar flowers: **d**, *X. pubescens* on *Moringa oleifera*; **e**, *X. latipes* on *Calotropis procera*.

show flower fidelity, most species being non-tubular or papilionaceous, facilitating easy access to nectar. Plants with tubular flowers, except *T. stans*, show a short tube which seems to have no impact on bees visiting these flowers. In the case of *T. stans* which has a long tube, *Xylocopa* bees rob nectar by biting holes at the corolla base. Cup-shaped flowers like those in *C. religiosum* and *C. arborea* attract bees.

The flowers are actinomorphic with radial symmetry or zygomorphic with bilateral symmetry. *Xylocopa* bees mostly prefer zygomorphic flowers in which wastage of pollen and nectar rewards is low but with increased efficiency of floral fidelity. However, *Calotropis* species with special floral morphology, gynostegium and actinomorphy, and *Solanum* species with actinomorphic floral pattern allow *Xylocopa* bees in the process of pollination and forage collection. Other plant species with actinomorphy show adaptations to attract different insects and *Xylocopa* bees use them opportunistically.

Anthesis and forage production

Flowers must produce their nectar and pollen at different times of the day or season for the foragers to become con-

tinuously active (Figure 3). The flowers must also balance the amount of sugar and water in the nectar, so that on each foraging visit, the bee gets the required energy and water while foraging^{23,24} (Figures 4–6). With regard to *Xylocopa* bees, varying anthesis schedules are exhibited, being at late night in *C. arborea*, around midnight in *C. religiosum*, in the afternoon in *Crotalaria* species, day long in *A. salviifolium* and *Calotropis* species, and between early morning and forenoon period in other plant species. *T. stans* shows twin anthesis schedules, one during the forenoon period and another during the afternoon. Anther dehiscence in pollen plant species takes place at or after anthesis, and the pattern of nectar production in nectariferous plants also varies with species. *Xylocopa* bees adjust their forage pattern suitably and the nectar rewards are dependent upon the long or short tongue and nature of nectar production.

In the case of poricidal flowers which are usually nectarless, buzz or vibrational pollination takes place, in which the vibration causes pollen expulsion from the anthers leading to efficient pollen harvesting by bees as in *C. religiosum*, *Cassia* and *Solanum* species. The bees exhibit territorial foraging behaviour by chasing away the intruder foragers to utilize pollen from *Cassia* species and

Table 1. Habit, flowering season and floral characteristics of plant species utilized as food resources by large carpenter bees

Family	Plant species	Habit	Flowering period	Flower size	Flower type	Floral symmetry	Floral colour	Floral odour	Anthesis time (h)	Floral reward
Alangiaceae	<i>Alangium salviifolium</i> Wang	Tree	Mar.–Apr.	Large	Non-tubular	Actinomorphic	Cream	Odouriferous	Day-long	Nectar
Asclepiadaceae	<i>Calotropis gigantea</i> R.Br.	Shrub	Year-long	Medium	Non-tubular	Actinomorphic	White	Odouriferous	Day-long	Nectar
Bignoniaceae	<i>C. procera</i> (Ait.) R.Br.	Shrub	Year-long	Medium	Non-tubular	Actinomorphic	Purple	Odouriferous	Day-long	Nectar
	<i>Tecoma stans</i> HBK.	Tree	Sept.–Mar.	Large	Tubular	Zygomorphic	Yellow	Odourless	0500–0700	Nectar
Caesalpiniaceae	<i>Bauhinia purpurea</i> L.	Tree	Oct.–Dec.	Large	Non-tubular	Zygomorphic	Purple	Odourless	1500–1700	Nectar
	<i>B. racemosa</i> Lam.	Tree	Feb.–May	Large	Non-tubular	Zygomorphic	White	Odourless	0430–0530	Nectar
	<i>B. variegata</i> L.	Tree	Mar.–Apr.	Large	Non-tubular	Zygomorphic	Purplish-white	Odourless	0500–0700	Nectar
	<i>Cassia alata</i> L.	Shrub	Sept.–Feb.	Medium	Non-tubular	Zygomorphic	Yellow	Odourless	0400–0600	Nectar
	<i>C. auriculata</i> L.	Shrub	Sept.–Feb.	Medium	Non-tubular	Zygomorphic	Yellow	Odourless	0500–0700	Pollen
	<i>C. fistula</i> L.	Tree	Sept.–July	Medium	Non-tubular	Zygomorphic	Yellow	Odourless	0600–0800	Pollen
	<i>C. occidentalis</i> L.	Herb	July–Dec.	Medium	Non-tubular	Zygomorphic	Yellow	Odourless	0200–0300	Pollen
	<i>C. stamea</i> Lam.	Tree	Apr.–Nov.	Medium	Non-tubular	Zygomorphic	Yellow	Odourless	0600–0700	Pollen
	<i>C. tora</i> L.	Herb	Aug.–Dec.	Medium	Non-tubular	Zygomorphic	Yellow	Odourless	0300–0400	Pollen
	<i>Peltophorum pterocarpum</i> (DC.) Backer ex K. Heyne	Tree	Mar.–June	Medium	Non-tubular	Zygomorphic	Yellow	Odourless	0600–0700	Pollen
	<i>Cochlospermum religiosum</i> (L.) Alston	Tree	Sept.–Oct					Odouriferous	0700–1000	Pollen and nectar
	<i>Crotalaria laburnifolia</i> L.	Shrub	Jan.–Apr.	Large	Cup-shaped	Zygomorphic	Yellow	Odouriferous	2300–2400	Pollen
	<i>C. verrucosa</i> L.	Shrub	May–Dec.	Medium	Papilionaceous	Zygomorphic	Yellow	Odouriferous	1200–1800	Nectar
	<i>Gliricidia sepium</i> (Jacq.) Kunth ex Walp.	Tree	July–Dec.	Medium	Papilionaceous	Zygomorphic	Bluish-white	Odouriferous	1200–1700	Nectar
Lamiaceae	<i>Pongamia pinnata</i> (L.) Pierre	Tree	Jan.–Mar.	Medium	Papilionaceous	Zygomorphic	Purple	Odouriferous	0730–1600	Nectar
	<i>Tephrosia purpurea</i> (L.) Pers.	Shrub	Mar.–May	Medium	Papilionaceous	Zygomorphic	Purplish-white	Odouriferous	0700–1000	Nectar
	<i>Anisomeles indica</i> (L.) Kuntze	Shrub	Aug.–Dec.	Medium	Papilionaceous	Zygomorphic	Purple	Odouriferous	0500–0700	Nectar
	<i>A. malabarica</i> (L.) R.Br. ex Sims	Shrub	Oct.–Jan.	Medium	Tubular (short)	Zygomorphic	Purple	Odouriferous	0530–0730	Nectar
Lecythidaceae	<i>Careya arborea</i> Roxb.	Tree	Oct.–Jan.	Medium	Tubular (short)	Zygomorphic	Purple	Odouriferous	0100–0500	Nectar
	<i>Moringa oleifera</i> Lam.	Tree	Mar.–Apr.	Large	Cup-shaped	Actinomorphic	Creamy white	Odouriferous	2100–2300	Nectar
Moringaceae		Tree	Feb.–May	Medium	Non-tubular	Zygomorphic	White	Odouriferous	0530–0930	Nectar
			Sept.–Dec.							
Polygonaceae	<i>Antigonon leptopus</i> Hook. & Arn.	Climber	Year-long	Small	Cup-shaped	Actinomorphic	Purple and white	Odourless	0600–0800	Nectar
Solanaceae	<i>Solanum trilobatum</i> L.	Herb	June–Dec.	Medium	Non-tubular	Actinomorphic	Bluish-purple	Odourless	0400–0600	Pollen
	<i>S. surattense</i> Burm.f.	Herb	July–Sept.	Medium	Non-tubular	Actinomorphic	Bluish-purple	Odourless	0400–0600	Pollen
Verbenaceae	<i>Gmelina arborea</i> Roxb.	Tree	Feb.–Apr.	Large	Tubular (short)	Zygomorphic	Yellow	Odourless	0800–1100	Nectar
Zygophyllaceae	<i>G. asiatica</i> L.	Shrub	Feb.–Oct.	Medium	Tubular	Zygomorphic	Yellow	Odourless	0500–0600	Nectar
	<i>Tribulus terrestris</i> L.	Herb	Year-long	Small	Non-tubular	Actinomorphic	Yellow	Odouriferous	0600–0800	Nectar

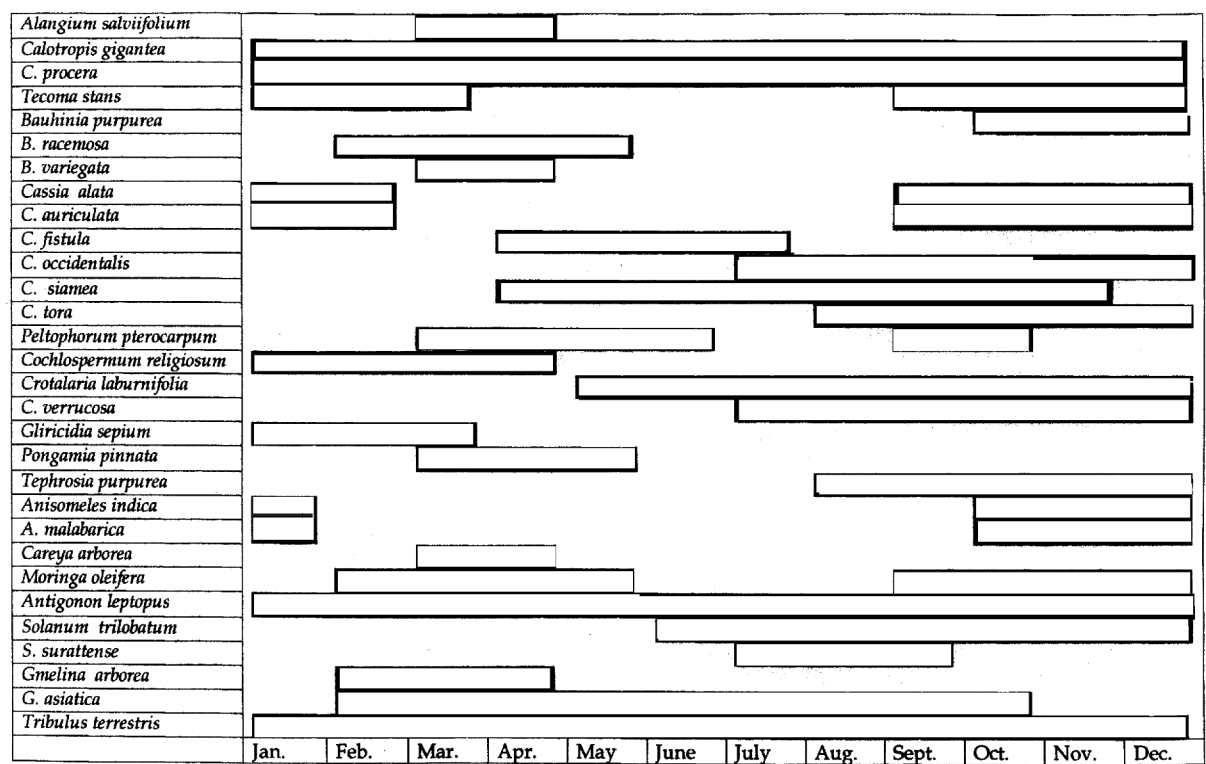


Figure 3. Flowering phenology of forage plants of carpenter bees.

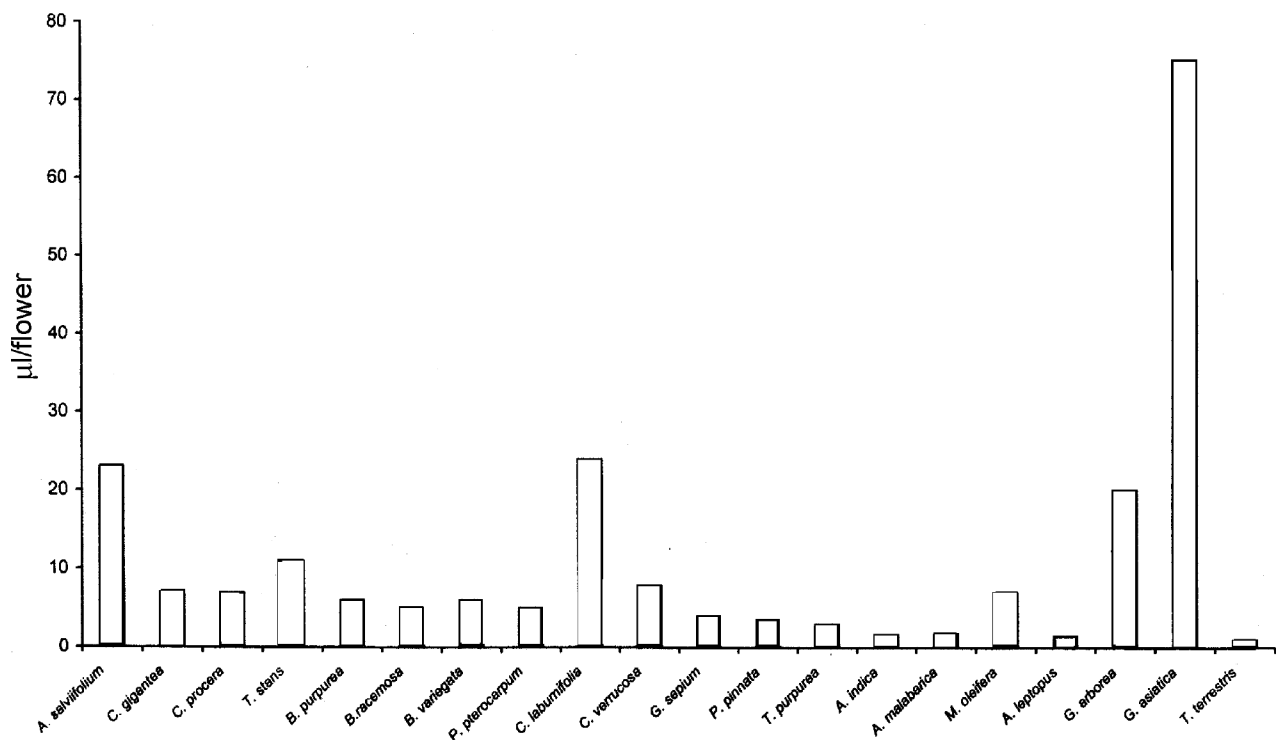


Figure 4. Average nectar volume per flower in some forage plants of *Xylocopa* bees.

nectar from *A. ilicifolius*, *A. salviifolium*, *A. malabarica* and *A. indica* depending on the abundance of standing forage

crop, at least for some period of time^{3,10}. Carpenter bees also show opportunistic foraging behaviour, which involves

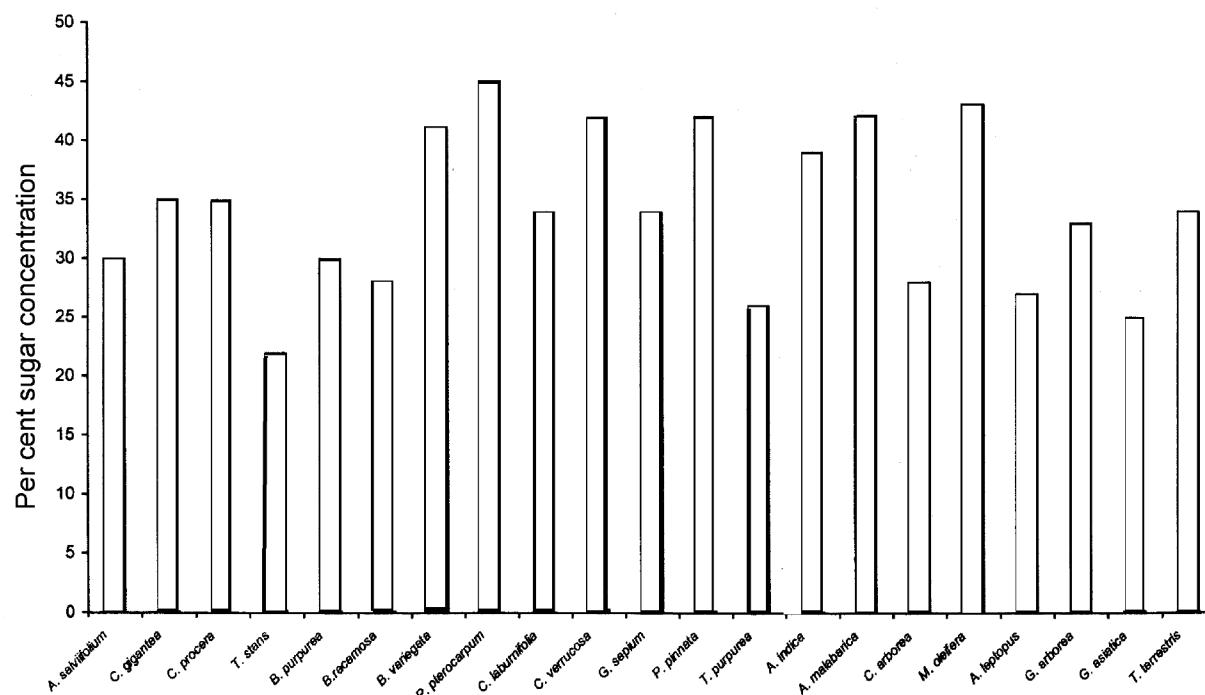


Figure 5. Average nectar sugar concentration per flower in some forage plants of *Xylocopa* bees.

utilization of appropriate and inappropriate flowers as an adaptive strategy to overcome food shortage as noted in *C. arborea*, *A. leptopus* and *T. terrestris*.

Xylocopa species have an important role in pollination in all plant species utilized by them as food resources (except *T. stans*), in which the *Crotalaria* species are most significant. The relationships between *Xylocopa* bees and most of the plant species are mutualistic for either food or for effecting pollination. The floral morphologies with certain characteristics appear to be adapted and co-evolved for pollination by carpenter bees.

Conclusion

Information available on the nesting ecology of large carpenter bees is scanty. Such information is quite fragmentary for *Xylocopa* bees other than *X. latipes* and *X. pubescens*. The nesting habits and nesting materials of carpenter bees from forests and other wild sources are being collected for fuel wood. Human interference and disturbance in such natural areas and in anthropogenic habitats is posing a threat to the survival of carpenter bees by the non-availability of nesting materials and shortage of food sources. In natural areas, these bees carry out an important function of decomposing and recycling the dead wood and soft stem materials but there is no such scope nowadays due to regular collection of such materials by humans. This situation suggests that further studies on the nesting ecology of *Xylocopa* bees are required to identify nesting materials in order to sustain them in the habitats where they flourish well.

Flower relationships of *Xylocopa* bees indicate that they are inter-dependent. Some plants are important as nesting sites, some others as pollen plants and several others as nectar plants. An extreme case of utilization of the same tree species, *C. siamea* for nesting and pollen collection by *Xylocopa* bees has been reported by Rashda³. In the absence of *Xylocopa* bees, most of the plant species adapted to pollination by *Xylocopa* bees do not fruit. The bees are quite plant-specific with regard to pollen procurement, important for brood-building. The scarcity of pollen plants in any habitat is bound to affect the number of generations per year and also health of the offspring of these bees. The number of nectar plants is also small and suggests that the bees are largely selective and utilize only some plants as nectar source. The flower relationships of *Xylocopa* bees in Visakhapatnam indicate that they utilize the same plant species (Table 1) for their food sources, although four hundred and forty-two dicotyledonous plant species occur in the area²⁵. This indicates that *Xylocopa* species have a short list of food plants and further studies in other parts of India will add some more food plants to the list. Such consolidated information is essential to prepare a floral calendar and sustain floral sources for use by *Xylocopa* bees throughout the year. The scattered or non-occurrence of these food plants affects the perpetuation of these bees greatly. In line with this, the production of two generations per year has been reported for the multivoltine *X. latipes* and *X. pubescens* in Visakhapatnam, where their food plants with a small number of individuals have a scattered occurrence³. Similarly, plant species utilized by these bees may show low

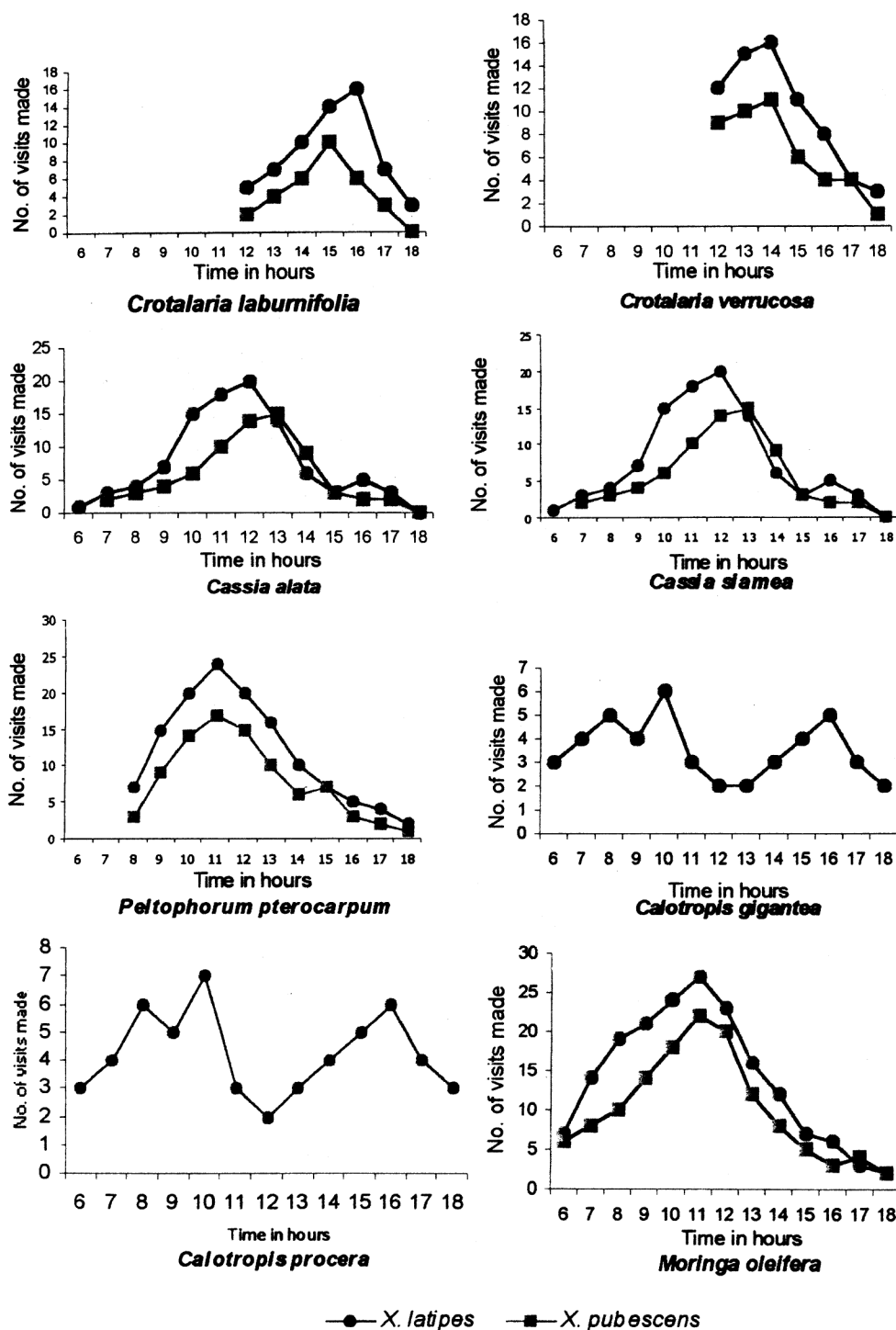


Figure 6. Hourly foraging activity of *Xylocopa* bees on some plant species.

or no fruit set rate, if not pollinated by them. These relationships are not just an indication of mutualism, but also a mechanism of perpetuation of plant diversity through *Xylocopa* pollination. Lane²⁶ and Moncks²⁷ reported that large carpenter bees are major pollinators of wild plants and several fruit and vegetable crops. Cervancia²⁸ showed that these bees are pollinators of many economic crops.

The introduction of carpenter bees is necessary to ensure adequate pollination for crops like cucurbits and passion fruit and also other fruit and vegetable crops. Carpenter bees are now mass produced in the Philippines for farm-pollination services. Further, carpenter bees are being managed by providing suitable nesting materials for pollination in passion fruit in USA, Brazil and Malaysia.

This is an evidence for the importance of carpenter bees in the reproduction of different plant species and thus for the production of plant biomass of terrestrial ecosystems, and for generating and maintaining genetic diversity of the plants. It suggests that there is an immediate need to carry out extensive studies on *Xylocopa*-flower relationships in India to have concrete information on the conservation and management of plant species, sustenance of *Xylocopa* bees and their field application as efficient pollinators in both natural and agricultural settings. Further, the bees hold promise as alternative pollinators in tropical and subtropical latitudes.

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