

## Review Article

# Large Carpenter Bees as Agricultural Pollinators

**Tamar Keasar**

*Department of Science Education—Biology, University of Haifa, Oranim, Tivon 36006, Israel*

Correspondence should be addressed to Tamar Keasar, tkeasar@research.haifa.ac.il

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Large carpenter bees (genus *Xylocopa*) are wood-nesting generalist pollinators of broad geographical distribution that exhibit varying levels of sociality. Their foraging is characterized by a wide range of food plants, long season of activity, tolerance of high temperatures, and activity under low illumination levels. These traits make them attractive candidates for agricultural pollination in hot climates, particularly in greenhouses, and of night-blooming crops. Carpenter bees have demonstrated efficient pollination service in passionflower, blueberries, greenhouse tomatoes and greenhouse melons. Current challenges to the commercialization of these attempts lie in the difficulties of mass-rearing *Xylocopa*, and in the high levels of nectar robbing exhibited by the bees.

## 1. The Role of Non-*Apis* Bees in Agricultural Pollination

Insect pollination of agricultural crops is a critical ecosystem service. Fruit, vegetable or seed production from 87 of the 115 leading global food crops depends upon animal pollination [1]. The value of insect pollination for worldwide agricultural production is estimated at €153 billion, which represents 9.5% of the value of the world agricultural production used for human food in 2005 [2]. The area cultivated with pollinator-dependent crops has increased disproportionately over the last decades, suggesting that the need for pollination services will greatly increase in the near future [3]. This contributes to the concern to beekeepers, growers of insect-pollinated crops, and policy-makers over recent widespread declines in honey bee populations (Colony Collapse Disorder) [4–6].

Wild and domesticated non-*Apis* bees effectively complement honey bee pollination in many crops [7, 8]. Examples of management of non-*Apis* species for agricultural pollination include the use of bumble bees, primarily for the pollination of greenhouse tomatoes, the solitary bees *Nomia* and *Osmia* for the pollination of orchard crops, *Megachile* for alfalfa pollination, and social stingless bees to pollinate coffee and other crops [9–12].

This paper focuses on the large cosmopolitan genus *Xylocopa* as an additional provider of agricultural pollination

services. Aspects of these bees' life-history, social organization, and foraging ecology are discussed in the context of their potential role as crop pollination agents.

## 2. The Biology and Life History of Carpenter Bees

Large carpenter bees belong to the tribe Xylocopini within the subfamily Xylocopinae (Hymenoptera: Apidae). They are currently grouped into a single genus, *Xylocopa* [13]. The genus comprises at least three clades [14] and ca. 470 species [15]. Carpenter bees occur in tropical and subtropical habitats around the world, and occasionally in temperate areas [16]. Biogeographical analyses suggest that the genus probably has an Oriental-Palaearctic origin, and that its present world distribution results mainly from independent dispersal events [14].

As implied by their name, carpenter bees dig their nests in dead or decaying wood, except for the subgenus *Proxylocopa* that nests in the soil [17]. The wood-nesting carpenter bees construct two main types of nests: (i) unbranched (also called linear), with tunnels extending in either one or both directions from the nest entrance. Linear nests are usually constructed in hollow or soft-centered plant material, such as reeds; (ii) branched nests (>2 tunnels), usually constructed in tree trunks or timber [18]. The type of nest constructed usually varies with species, but some species show plasticity

in nest architecture, depending on the nesting substrate available to them [19]. The nesting female lays one or a few eggs along a tunnel during a brood cycle, provisions them, and constructs partitions of masticated wood to separate the offspring from one another. Maternal care in carpenter bees also involves guarding of the immature offspring and feeding of the newly matured ones by trophallaxis [20–22]. In some species, helper females participate in offspring care rather than nesting independently, thus nesting can be social (see below). Some species are univoltine, whereas others produce more than one brood per year [19]. The activity season of carpenter bees spans 8–12 months, depending on species (e.g., [21, 23–25]). Carpenter bees in temperate areas hibernate during the cold season [19, 26], but emerge to forage on warm winter days [21, 23].

The mating behavior of carpenter bees has been described for 38 species belonging to 16 subgenera [27]. Variation in mating strategies among subgenera has been recorded. In some subgenera, males search for females at nesting sites, flowers, or landmarks (non-territoriality). In others, they monopolize resources used by females, such as flowers or nesting sites (resource-based territoriality). Males may also monopolize areas lacking resources for females (non-resource-based territories, or leks) [18, 28]. A phylogenetic analysis suggests that resource defense is the ancestral state, and that this mating system is correlated with low color dimorphism between males and females and a small size of the mesosomal pheromonal gland [27].

Territorial males chase away intruding males [28, 29], which they identify by sight and by the odor emitted from the intruders' mandibular glands [30]. They also use a pheromone secreted from their mandibular gland to mark their territory [30]. When females enter the territories, males follow and try to mount them [28, 31]. Observations of copulations in carpenter bees are extremely rare [28] and were recorded only for a handful of species. In *X. varipuncta*, matings take place in the non-resource territories [32], while in *X. sulcatipes* and *X. flavorufa*, they occur at high elevation during flight [21, 31, 33].

### 3. Social Organization

Sociality, involving non egg-laying guard bees and a dominant egg-laying forager, has been described for ten species of *Xylocopa*. In nests of the African species *X. combusta*, first eclosing daughters remain in their natal nests and perform guarding duties while their mothers produce a second brood ([34] cf. [22]). Similarly, in nests of *X. pubescens* sociality generally occurs after the emergence of the young, where either the mother is the reproductive and a daughter guards or vice versa [20, 35]. Matrifilial nests of *X. virginica* (comprised of a mother and her daughters) also show reproductive skew, and guarding individuals become reproductive in the following year. In these nests, the mother performs all nest maintenance, foraging, cell preparation and oviposition, whereas the younger inactive females only perform guarding duties [36]. Nests of *X. sulcatipes* can be matrifilial, composed of sisters, or involve the joining

of unrelated females [21, 37]. Some *X. sulcatipes* nests are initially quasisocial (no reproductive division of labor), but after a brief period of reproductive competition involving oophagy, a division of labor is usually established. Eventually most nests contain one reproductive and a guard [38]. The helping role of female offspring has been suggested to promote greater maternal investment in daughters than in sons, leading to the female-biased sex ratio recorded in *X. sulcatipes* [37]. In both *X. pubescens* and *X. sulcatipes*, the reproductive females produce 100% of the offspring while the guards produce none [39].

Nests of *X. sonorina* also exhibit high reproductive skew, where the forager (mother) reproduces and feeds nestmates via trophallaxis, and additional females (daughters and/or joiners) share guarding duties [40]. For *X. frontalis*, *X. grisescens*, and *X. suspecta* matrifilial, semisocial, and communal nests have been recorded [41]. Genetic analysis of *X. aeratus* and *X. bombylans*, which form multi-female nests during part of the breeding season, indicated the presence of multiple matrilineal lines in approximately 50% of nests. Socially nesting females were frequently sisters in one of the populations studied, and were often unrelated in a second population. The results also indicated that temporary high reproductive skew occurred in multi-female nests, that is, that different females were reproductive during different parts of the season [22].

Several ecological and life-history variables were suggested to promote social nesting in carpenter bees. Social living was found to correlate with late season [42] and older age [35] in *X. pubescens*, possibly because matrifilial nesting only occurs when mothers produce their second brood. Nest structure was proposed as an additional factor that affects social organization: in some species, females in branched nests build and provision separate tunnels at the same time, which can result in a communal social organization. In other species, females construct one tunnel for the first brood generation and only construct a new tunnel after the first brood has reached maturity. This can then result in eusocial nesting, where the daughters of the first generation assist their mother in building and provisioning subsequent tunnels [19]. Finally, a period of reproductive inactivity of mature offspring was proposed as a transition step toward social living. Such a period occurs in some solitary species (such as *X. frontalis* and *X. grisescens*), where newly emerged adult females remain in their natal nest for 20–30 days. During this time, they are provisioned by their mother or by their oldest sister, if the mother is absent. In some species, this association becomes permanent in a fraction of the nests (e.g., in *X. suspecta* [25]), which then become social.

Improved defense against parasites and predators has been suggested to favor the evolution of social nesting in bees (e.g., [43]). Carpenter bee nests are attacked by several types of natural enemies, including parasitoid wasps and flies, predatory wasps, ants, termites, and insectivorous birds [21, 44]. However, in *X. pubescens*, the frequency of parasitism did not differ between social and solitary nests [45]. Thus the role of guards in reducing nest parasitism is not supported so far.

The most extensive work on the consequences of sociality has been carried out for *X. pubescens*. In this species, the

frequency of social nesting increases as the reproductive season progresses. It has been suggested that this increase has evolutionarily been imposed on females by shortage in nesting sites [20]. Social nesters spend more time foraging outside their nests as compared with solitary individuals, perhaps because the presence of the guard in the nest reduces the risk of prolonged foraging [46]. Social nesters also suffer fewer nest takeovers by intruders than solitary nesters, providing a possible benefit for social nesting when competition for nests is high. The guards, in turn, may benefit from increased indirect fitness (if related to the reproductive), and increase their chances of eventually taking over the nest [46]. Thus, social organization can affect the fitness of *X. pubescens* females. Social and solitary nesters that foraged within a greenhouse differed in their food-plant preferences. Social females directed more of their foraging to a pollen source (*Portulaca oleracea*) than solitary nesters, possibly because of their higher brood production rates [47].

## 4. Foraging Ecology

**4.1. Abiotic Requirements for Foraging.** Carpenter bees tolerate high ambient temperatures during foraging, and most species are inactive at low temperatures. For example, the lower activity temperature thresholds are 23°C for *X. capitata* [48], 21°C for *X. sulcatipes*, and 18°C for *X. pubescens* [21]. Flower visit rates in *X. olivieri* are highest at a combination of high (25–35°C) temperatures and low (1–100 Lux) illumination levels [17]. *X. arizonensis* individuals that foraged on *Agave schottii* together with honey bees and bumble bees were active mainly during the late morning hours, while honey bees and bumble bees were more crepuscular. These patterns were suggested to reflect low competitive ability, together with high thermal tolerance, in the carpenter bees [49]. *X. varipuncta* maintains flight activity within an ambient temperature range of 12–40°C [50]. This heat tolerance suggests good heat regulation ability in carpenter bees, possibly controlled by a thermoregulatory center in the prothorax [51].

The activity period of some species, for example, *X. sulcatipes*, *X. cearensis*, and *X. ordinaria*, spans most of the daylight hours [21, 52, 53]. In other species (such as *X. pubescens*, *X. tabaniformis*, and *X. olivieri*), activity is crepuscular [17, 21, 54, 55]. A few species are nocturnal: *X. tenuiscapa* forages on its pollen host on moonless nights [56], and *X. tranquebarica* [57] has been observed foraging on moonlit nights.

**4.2. Water Balance.** Carpenter bees often ingest excess water during nectar foraging. Analysis of nectar consumed by *X. capitata* showed that it is very concentrated. Nevertheless, their hemolymph is only moderately concentrated, and their urine is very dilute. This suggests that ions, rather than water, may be limiting for carpenter bees [58]. This hypothesis is supported by the observation that bees often excrete water before and during flight, and that they often engage in water evaporation from ingested nectar [59]. A similar excess of water ingestion, which leads to copious excretion

and evaporation of water, was described for *X. pubescens* foraging on the nectar of *Callotropis*. On the other hand, physiological water requirements are finely balanced with the water contents of *Callotropis* nectar in the sympatric species *X. sulcatipes*, possibly due to extended coevolution with this plant [59].

**4.3. Nectar Robbing.** Nectar-foraging carpenter bees often perforate the corollas of long-tubed flowers, and thereby reach the nectaries without contact with the anthers. Such “illegitimate pollination” or “nectar theft” has been reported for *X. virginica* and *X. micans* foraging on blueberries. Nectar robbing in blueberries may reach 100% of the visits [60] and significantly reduces fruit set and seed number as compared with plants visited by honey bees ([61], but see [62]). Nectar robbing by carpenter bees has also been observed in the wild plants *Petrocoptis grandiflora* [63], *Fouquieria splendens* [64], *Glechoma longituba* [65], and *Duranta erecta* [66]. Corolla tube perforation contributed to the reproductive success of the plants in *P. grandiflora* and *F. splendens*, indicating that the nectar robbers were dusted with pollen during foraging, and functioned as pollinators. In *G. longituba* and *D. erecta*, on the other hand, nectar robbing by carpenter bees reduced seed set, as compared with plants visited by legitimate pollinators [63–66].

**4.4. Food Sources.** Carpenter bees in natural habitats are generalist nectar and pollen foragers. For example, foraging *X. cearensis* were recorded from 43 plant species in Bahia, Brazil [52], while *X. latipes* and *X. pubescens* foraged on 30 species in India [67]; In Israel, *X. pubescens* and *X. sulcatipes* used 61 species as forage plants [21]; *X. darwini* in the Pacific is known to visit the flowers of 79 plant species [29]; 28 plant species provide nectar and pollen for *X. ordinaria* in Brazil [53].

Carpenter bees can also be trained to collect sucrose solution from feeders in experimental settings. In laboratory experiments, *X. micans* were able to discriminate between sucrose solutions that differed in mean volume (1 versus 3 microliter) and concentration (10% versus 30%). They were indifferent to variability in both nectar volume and nectar sugar concentrations. This risk indifference was recorded if the bees were fed or starved [68].

## 5. Crop Plants That Are Pollinated by Carpenter Bees

Carpenter bees pollinate passionflower (*Passiflora* spp.) in their native habitats [69] and in commercial agricultural settings [70–73]. They provide better pollination service than honey bees for this crop [71]. *Xylocopa* subgenus *Lestis* has been successfully reared in greenhouses for tomato pollination in Australia. Their foraging activity led to an increase in tomato weight by 10% relative to a combination of wind and insect pollination. The efficiency of carpenter bees in pollinating tomatoes is increased by their ability to buzz the anthers [9]. In a pilot study in Israel, the fruit set of greenhouse-grown honeydew melons was three times

higher when pollinated by *X. pubescens* compared to honey bee pollination [74]. Social and solitary nesters had similar efficiency in pollinating this crop: they did not differ in the daily activity patterns and flower visitation rates. Pollination by both types of nesters led to similar fruit sets, fruit mass, and fruit seed number [47].

Carpenter bees are important pollinators of cotton in Pakistan, India, and Egypt [33]. *X. varipuncta* is compared favorably with honey bees (*Apis mellifera*) as pollinators of male-sterile cotton in field cages in the USA [75]. However, *X. pubescens* in Israel did not provide satisfactory pollination of cotton for hybrid seed production (D. Weil, personal communication). Finally, the night-flowering cactus *Cereus repandus* (syn. *C. peruvianus*) is pollinated by *X. pubescens* in Israel [76].

## 6. Domestication and Mass Rearing of Carpenter Bees for Agricultural Pollination

A major obstacle to the commercial use of native pollinators in agriculture is the need to mass-rear them, rather than collect them from nature. Devising efficient and cost-effective mass-rearing protocols for *X. pubescens* is a necessary step in this direction. Attempts to mass-rear carpenter bees have focused on the construction of nest boxes that are placed in natural habitats to enhance nesting success. Skaife [77] constructed observation nests of bamboo tubes and transferred hibernating *X. caffra* into them. Most of the females remained in these nests after they exited hibernation. Oliviera and Freitas [78] designed and tested nest boxes for *X. frontalis*, based on the general design of Langstroth honey bee hives. Each of nine wooden frames in these boxes was modified to serve as an independent *Xylocopa* nest. Colonization rates of these boxes ranged from 19% to 52%, and the proportion of males in the emerging brood was 0.38. Efforts to develop protocols for captive mating and rearing of carpenter bees have so far met with limited success (unpublished results). The endocrine and molecular pathways that underlie reproduction in carpenter bees are yet unknown. Elucidation of these pathways will help identify the bottlenecks in the bees' reproduction, which may include overwintering of adults, mating, sperm storage and choice, nest construction and/or brood care. Information on the potential reproductive pitfalls, and their physiological mechanisms, is expected to facilitate the development of effective captive breeding methods for *Xylocopa*.

## 7. Conclusions and Future Prospects

Carpenter bees possess several advantages as potential crop pollinators compared to other non-*Apis* bees. Many solitary bees have a short activity season and/or are specialist foragers, and therefore do not provide a broad alternative to honey bee pollination. Carpenter bees, on the other hand, have long activity seasons and feed on a wide range of plant species. In addition, they are capable of buzz-pollination. This makes them potentially more versatile as agricultural pollinators. Hibernation occurs in the adult

stage, and females start foraging whenever temperatures reach high enough values. This means that it is relatively easy to manipulate the onset of foraging in greenhouses. Another important advantage is that the genus has a worldwide distribution. This implies that local species of *Xylocopa* can potentially be used over wide areas, reducing the need to import exotic pollinators. The possibility to lure these bees into suitable artificial nesting material allows provisioning of nesting material that can be easily used in agricultural settings and moved to places where pollination services are needed [79].

In spite of higher per-capita pollination efficiency in some crops, carpenter bees are clearly inferior to honey bees in terms of pollinator work force, as they do not form large nests. Therefore they are expected to contribute most to crop pollination when honey bees are ineffective. For example, the high thermoregulatory ability of carpenter bees enables them to forage at higher ambient temperatures than honey bees. This makes them attractive candidates as pollinators in hot areas and in hot microclimates, such as in glass houses. The crepuscular and nocturnal activity of some species may also allow them to pollinate night-flowering crops, which are not visited by honey bees.

Several problems remain in the management of carpenter bees for crop pollination, which call for further research. Most important is the need to develop an efficient captive breeding program for carpenter bees, which would include controlled selection of genotypes, mating, and nest founding. Such protocols have already been developed for other non-*Apis* pollinators, such as *Osmia lignaria* [80] and *Osmia cornuta* [81]. They include guidelines for nest construction and placement, overwintering and transportation of the bees. A complementary challenge is to enhance reproduction of wild *Xylocopa* populations, through provisioning of nesting material to their natural habitat. The availability of nesting resources was shown to correlate with the community structure of wild bees [82]. Moreover, experimental enhancement of nest site availability has led to dramatic increases in wild populations of *Osmia rufa* [83]. These findings suggest that *Xylocopa* populations, and the pollination services they provide, may also benefit from nest site enhancement in agroecosystems. Additional information about the pathogens and parasites of the genus is needed as well [84]. A combination of ecological, physiological, and molecular genetic studies is likely to provide these essential data.

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