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Small Carpenter Bees (*Ceratina*)

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The small carpenter bees comprise the single genus *Ceratina* of the tribe Ceratinini (Xylocopinae: Apidae). They are represented by approximately 200 described species with a global distribution spanning all habitable continents and ecoregions. *Ceratina* are stem-nesting bees with a broad range of social behavior from solitary and ▶ subsocial to ▶ semisocial and ▶ eusocial colony organization. As in other xylocopine bees, the adult life span of *Ceratina* is unusually long, a life history trait that strongly influences their social behavior. Their phylogeny, biogeography, and nesting biology are well understood. *Ceratina* are foundational in our understanding of maternal care, mutual tolerance, and division of labor in facultatively social insect societies.

Nesting Biology

Ceratina nest in dead broken stems of pithy plants (Fig. 1). Females typically disperse from the natal nest to establish new nests solitarily, although sometimes females will reuse their nest and can form cooperative colonies with a reproductive division of labor [2]. Nests are formed in a linear burrow. Pollen is collected to form a mass provision onto which an egg is laid before the brood cell is capped by scraping pith from the interior walls of the nest to form a partition. This process is repeated in a serial manner during brood establishment, after which females remain in the nest entrance to guard and care for offspring during development. Females break down the partition to groom the offspring, a very unusual behavior. The mass provision provided to the egg is all the nutrition required for an egg to develop into an adult (Fig. 2), but mothers remain on the nest providing prolonged maternal care allowing for mother-offspring interaction. This subsocial behavior distinguishes *Ceratina* from most other solitary bees. Females guard the nest and produce a yellow mandibular secretion with a strong citral odor that they smear around the nest entrance to deter off predators. Maternal guarding and inspection of brood cells each evening are thought to reduce parasites, and routine grooming removes fungal infection of developing brood. The linear nest architecture in pithy stems prevents large colony formation. Nests are solitary or subsocial if attended by a single adult female. Semisocial and primitive eusocial colony organization is observed when typically two, but sometimes three females remain in a reused nest. As more *Ceratina* species are studied, we are finding that there is a range of social behaviors

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Small Carpenter Bees (*Ceratina*), Fig. 1 The Australian small carpenter bee *Ceratina australensis* nests in dead pithy stem of fennel. Note brood cell partitions made from scraping the lumen of the nest to form partitions between broods. The mother (left) is in the nest gallery guarding her offspring. The bee offspring (center) is a pupa about a week away from eclosion. The wasp pupa (right) reveals that a parasite entered the nest while the mother was out foraging and laid its eggs in the nest

Small Carpenter Bees (*Ceratina*), Fig. 2 Development of the common eastern North American small carpenter bee *Ceratina calcarata*. Mothers forage and produce a mass provision on which an egg is laid (top left). The egg hatches into a larva, consuming the pollen mass to become a pre-pupa (top right). The pupa starts off completely white and gains eye pigmentation followed by body pigmentation until the final molt when the adult bee emerges (bottom right)

and more diversity in their habitats and nesting biology than previously thought.

Social Behavior

Ceratina species produce a single brood per year in temperate regions and multiple broods per year in tropical ranges. In temperate species, the single brood per year limits *Ceratina* to solitary and subsocial colony organization. Adult females in temperate regions typically live only 12–16 months, an unusually long time compared to most bees, but not long enough for the formation of complex social colonies. Faster brood developmental and prolonged foraging opportunities in the tropics allow for two or more generations per year. Bivoltinism (two generations per year) or multivoltinism (> two generations per year) allows females the option of dispersing to establish nests solitarily or remaining in the natal nest, sometimes with kin, to establish social colonies.

Small Carpenter Bees (*Ceratina*), Fig. 3 Maternal manipulation to produce dwarf eldest daughters in the common eastern North American small carpenter bee (*Ceratina calcarata*). The dwarf eldest daughter (left) is the product of under-provisioning by her mother (right) resulting in small adult body size followed by physical coercion to force this worker daughter to forage and feed her siblings

Ceratina tend to have small colonies with one to two adult females and 5–10 offspring per season. Colony sizes rarely reach 20 or more brood in one stem. The small colony sizes of *Ceratina* led early researchers to regard this genus as solitary [7], but later studies revealed widespread group living [6].

Recent studies on the temperate North American species *C. calcarata* have revealed that prolonged maternal care and mother-offspring interaction are necessary for the survival of adult brood over the wintering [9]. Further studies have revealed the role of maternal aggression, nutritional manipulation, and maternal quality on the social behavior of this species. Forced association studies in laboratory experiments have shown *C. calcarata* are capable of more complex social behaviors than are normally observed in the wild. Ephemeral nesting substrates and univoltine colony cycles preclude comparable behaviors from being observed in the wild.

Molecular phylogenetics of the small carpenter bees indicate an African origin, where they were likely social, followed by rapid radiation around the globe [3]. Small carpenter bees are speciose on all continents except Australia, where there is just one species, *C. australensis*. This species is facultatively social, with both solitary and social colonies together in the same populations. Social colonies are semisocial, as they form between sisters remaining at the natal nest. Although genetic data on the relatedness of social colony formation are few, behavioral studies of Japanese congeners have observed eusocial and semisocial colony organization in species at low latitudes [8].

Reproductive Castes

Reproductive division of labor is observed in all social colonies of the small carpenter bees. Age- and size-based dominance hierarchies have been observed in eusocial species, although the mechanism of division of labor remains unknown in age- and size-matched semisocial societies. In eusocial colonies, the mother is typically the reproductive dominant, monopolizing reproduction and policing any egg-laying attempts by daughters by eating their laid eggs (oophagy) [8].

In North American *C. calcarata*, mothers may rear a female offspring in the first brood cell position and under-provision this daughter to produce a dwarf first daughter (Fig. 3). Upon eclosion, this first daughter carefully crawls past her unemerged siblings, rebuilding brood cell partitions as she goes, and is met by her mother in the nest gallery. Mothers will then nudge the dwarf daughter into foraging for and feeding her adult siblings as they emerge. Additional feeding of regular adult offspring is necessary for their overwintering survival, as

they remain in their natal nest until the next spring. Dwarf eldest daughter production and sibling care are also reported in multiple Japanese congeners [4].

An unusual case of sociality occurs in the Australian *C. australensis* [5]. Two-female colonies are formed in which one individual (the social primary) monopolizes foraging and reproduction, while the other (social secondary) remains in the natal nest as a guard. Nest sites are not limiting, and per capita brood production is greatly reduced in social compared to solitary nests. There is thus no benefit to the social primary in retaining a social secondary, and the secondary female incurs greatly reduced fitness compared to solitary females in the population. It is consequently thought that severe parasite pressure may select for this helping behavior, since secondaries protect social colonies from the total nest failure observed in parasitized solitary colonies. This form of bet-hedging has been proposed for the long-term maintenance of social nesting despite observed short-term reduced fitness returns due to the unpredictability of selective environments.

Sex Allocation

Ceratina sex ratios vary among populations and seasons, and there is evidence that maternal body size may influence investment strategies. Sex ratios are typically 1:1 at the population level in *C. calcarata*, but reproductive females can skew investment from all-female to all-male. (As in all hymenopterans, ▶ haplodiploid sex determination allows the female to determine the sex of each offspring.) Males are the smaller sex and thus require less provisions than females. A male numerical sex ratio bias balances the female-biased cost ratio. Large females produce larger clutch sizes, offspring of larger body size, and female-biased sex ratios and invest in dwarf eldest daughters. Smaller mothers, by contrast, produce small clutch sizes, small offspring, and male-biased broods and forgo dwarf eldest daughter production [9]. Female-biased sex ratios are reported in various bivoltine species [2]. The most likely source of these female-biased ratios is their mating biology. If males from one generation survive long enough to mate with females of the next generation, then the reproductive value of males is greater than indicated purely from their numerical investment, thus selecting for a greater investment in female offspring [1].

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