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**Research article**

# Sociality in *Euglossa* (*Euglossa*) *viridissima* Friese (Hymenoptera, Apidae, Euglossini)

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**Abstract.** *Euglossa viridissima* is an orchid bee that forms both solitary and multiple female nests, making it a suitable species for the study of factors leading to diverse degrees of sociality in Euglossines. We conducted observations in eight reused nests (where a first generation of bees had been produced) kept in artificial boxes from the Yucatan Peninsula, Mexico. Five nests were reused (reactivated) by a single female (SFN), two nests reused by a mother and one daughter (MFN1) and one nest reused by the mother and two daughters (MFN2). No single nest was reactivated by unrelated females. The number of foraging trips, their duration and the duration of cell provisioning was not different between SFN and MFN. The overall production of cells per female was not different either between both types of nest. However, in MFN although all females did lay eggs, there was a reproductive skew in favor of the mother (95 and 45 % of the brood produced in MFN1 and MFN2 respectively). She showed reproductive control of her daughters through oophagy and displaying threatening behavior when the daughters tried to open a cell where she had laid an egg. Brood losses to parasites (*Anthrax sp.* (Bombyliidae) and *Hoplostelis bivittata* (Megachilidae)) were only found in SFN which possibly reflects and advantage of MFN in this respect. Our results coupled with other studies in *Euglossa,* reveal that a wide range of social behaviors occur in this genus, from solitary and communal to primitive reproductive division of labor. Multiple factors involving different levels of pressure imposed by food availability and parasites may favor such a diverse range of nesting behaviors. Interestingly, female associations in *E. viridissima* seem a result of kin selection that is enforced by coercion from mother females on their daughters. More studies are needed to shed light upon the social organization of *Euglossa* and other Euglossines and on their phylogenetic relationships in order to trace the origins of eusociality in Apidae.

*Keywords: Euglossa*, sociality, kin selection, female parasitism, Yucatan.

## Introduction

Orchid bees (Euglossines) are amongst the most important bees of the Neotropics, most notably because they act as pollinators of orchids and several other families of plants, thus playing a key role in the conservation of tropical habitats (Cameron, 2004; Roubik and Hanson, 2004). Together with honey bees (Apini), stingless bees (Meliponini) and bumble bees (Bombini), Euglossines form the clade of corbiculate Apidae (Michener, 2000). Interestingly, within the corbiculate Apids, Euglossines are the only group that is not clearly eusocial, with some species being solitary or with primitive forms of sociality (Michener, 2000).

*Euglossa* is the largest and most widely distributed genus amongst Euglossines, with 43 species out of the 100+ identified so far, occurring in México and Central America (Roubik and Hanson, 2004). In spite of their importance as pollinators, very few studies have been conducted on the biology of these tropical organisms because specimens and the nests of most species are difficult to trace (Ramirez et al., 2002). The descriptions so far available indicate that most species of *Euglossa* are solitary although the occurrence in some species of multiple female nests suggests sociality may be found within the genus (Cameron, 2004).

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As a rule, in *Euglossa* nests seem to be established in all cases by a solitary female but these can be reused by succeeding generations (reactivation), thus originating nests with several females occurring at one time (Augusto and Garófalo, 2004). Alternatively, nests may be shared by unrelated individuals (Garófalo et al., 1998). Despite of reports on multiple female nesting in *Euglossa* (c.17 species out of over 100 identified), nesting biology and interaction amongst females has only been reported for *E. cordata* (Augusto and Garófalo, 1994), *E. atroveneta* (Ramírez-Arriaga et al., 1996), *E. annectans* (Garófalo et al., 1998), *E. fimbriata* (Augusto and Garófalo, 1998), *E. truncata* (Braga and Garófalo, 1998), *E. hyacinthina* (Soucy et al., 2003), and *E. townsendi* (Augusto and Garófalo, 2004). However, the limited description in numbers of species and nests per species has prevented a better understanding of the distribution of sociality and its causes in *Euglossa* and the interactions that occur amongst females inhabiting the nests.

Preliminary observations in *E. viridissima* from the Yucatan Península of México have revealed that solitary (SFN) and multiple female nests (MFN) exist in this species and that occupation of cavities occur across the whole year (González and Paxton, 2001; Cocom et al., 2005). Such characteristics make *E. viridissima* a suitable species for the study of behavioral patterns and factors leading to diverse degrees of sociality in Euglossines

The use of artificial cavities has been suggested as a feasible method to increase the number of nests studied and conduct more detailed observations on the social interactions that occur in multiple female nests (Garófalo et al., 1993; Cameron, 2004). In the Yucatan Peninsula, *E. viridissima* builds nests in artificial lodgings that can be easily relocated, allowing marking of bees and cells to analyze in detail the process of nest founding and female interactions (González and Paxton, 2001). The females of *E. viridissima* are robust, medium sized bees (3–4 mm wide, 11–13 mm long), bright metallic green colored, and the male has a characteristic cushion of white hairs on the second sternum (Roubik and Hanson, 2004). This species is common across Mexico and most of Central America and recorded from near sea level up to 1,900 m.a.s.l. (Ramírez et al., 2002).

The following questions were proposed with the aim of documenting if this species shows evidence of sociality in MFN: 1) Is there evidence of tolerance amongst females in *E. viridissima?* 2) Are the bees genetically related? 3) Does division of labour occur in such type of nests? 4) Is there evidence of reproductive dominance? 5) What are the likely advantages for MFN in this species? The answers to these questions may provide additional evidences to test hypothesis on the social evolution of bees.

## Materials and methods

This study was conducted at the Department of Apiculture of the Campus of Biological and Animal Husbandry Sciences, Universidad Autónoma de Yucatan in Xmatkuil, Mexico (89.37°W, 20.52°N). This region has a sub tropical climate with a rainy season during the summer (García 1981). The average annual temperature is 26.8 °C and the average rain fall is 984.4 mm and 80 % of the rain occurs during the period of May to October (Duch, 1988). The vegetation type is that of a tropical deciduous forest (Flores and Espejel, 1994).

Wooden boxes (7x3x3 cm) with an inner layer of wax and stingless bee cerumen were placed monthly in the stingless bee house at the Campus from which 22 nests were recovered. The observations concentrated on the nests that were reused (reactivated nests), after first generation of bees had been produced. A glass sheet was placed as an inner cover on the boxes and allowed observation of the behavior of the female (s) in the nests without disturbance. All the individuals were marked on the thorax soon after emerging from their cells by taking the box to a dark room and manipulating the bees under red light.

The observations were conducted for 11 hours per day between 07:00 to 18:00 hours. The observations in the nests included the whole process of reactivation, including the preparation of old and new cells, the oviposition process and cell sealing and the foraging trips. The total number of cells per nest was counted and a map of their position in each nest was drawn. During this period, the number and duration of each trip performed during the provisioning of food of a single cell were recorded. Detailed observations on the behavior of the females during cell provisioning and oviposition were conducted to determine if there was evidence of division of work and reproductive dominance by either of the females. Data on the number and duration of foraging trips per cell and the number of cells produced per female in single and multiple female nests were compared using the Mann-Whitney *U* tests to determine the source of significance (Zar, 1999).A detailed record of each cell allowed the detection of parasites and parasitized cell rates between reactivated nests with single and multiple females were assessed by a contingency table Chi-square test (Zar, 1999).

All mean values were expressed ± one standard deviations, and a probability value (P value) $< 0.05$ was considered significant. All statistical analysis were performed using SPSS 11.0 for Windows (SPSS Inc., Chicago, IL).

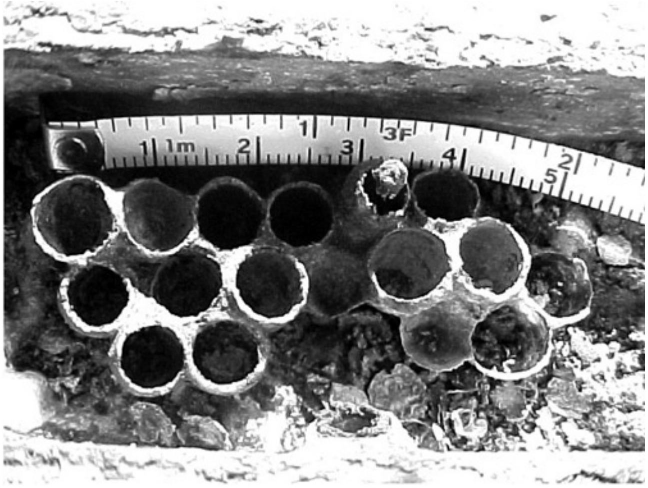

**Figure 1.** Top view of a reactivated nest of *Euglossa viridissima* established in a wooden box showing nine new cells (left) clumped next to the remaining of the old ones that have also been enlarged.

## Results

Twenty two nests were established in the artificial boxes (between May 2004 to March 2005) from which eight nests (36.3 %) were reused (reactivated). Two types of nest reactivation were observed (according with Augusto and Garófalo, 2004): 1) reactivation by a single female (SFN) in the absence of the mother (observed in five nests) and 2) reactivation by one or more females in the presence of the mother (MFN) of which two nests were reactivated by one female in the presence of the mother (MFN1) and one nest was reactivated by two females in the presence of the mother (MFN2) (37.5 % of the reactivated nests had multiple females).

The phase of cell construction and provisioning did not show differences between SFN and MFN. On average, the number of trips that the females made for provisioning a single cell was 9.6±1.1 (n=18) in SFN and 9.8± 2.2 (n=18) in MFN (Mann-Whitney test, Z= -0.16, P= 0.88). Each trip lasted in average 76.2±13.6 min (n=20) in SFN and 79.0±24.5 min (n=23) in MFN (Mann-Whitney test, Z= -0.13, P= 0.89). The duration of cell provisioning was also similar (Mann-Whitney test, Z= 1.33, P= 0.19) between SFN (24.8±1.8 h; n=16) and MFN (25.7±1.8 hours; n=18). In MFN the daughters reused the cells built by the mother but also built new ones (Fig. 1). The average number of cells built in SFN was 8.2±3.1 and each was constructed in contact with others forming different rows (Fig. 1). In the two MFN1 (mother and one daughter) the total number of cells was 15 and 18 respectively. In the MFN2 nest the number of cells reached 26. Thus, there was an increase in the absolute number of cells in the case of MFN compared to SFN but not in the number of cells per female which was 8.2±3.1 in the latter compared with 8.25±0.9 in MFN1 and 8.6 in MFN2. Nevertheless, since the mother prevented daughter reproduction, her net production of brood was substantially higher in MFN (see below).

In both, MFN1 nests, only the daughter females did foraging trips whilst the mother remained in the nest all the time. In the MFN2 nest each daughter built and provisioned individual cells and they did not collaborate in this process. The mother did not participate in the building and provisioning of the new cells and she only elongated the cell (which was also performed by the daughters) after provisioning finished, just before egg laying. The elongation of the cells by the mother occurred when her offspring were outside foraging.

**Figure 2.** A mother *Euglossa viridissima* (top) opens a cell before eating her daughter's egg in her presence.

Nineteen ovipositions were observed in detail in the MFN1 nests. In 9 of them the daughter laid an egg and finished sealing the cell, the process took 558±231 seconds. After this, the mother in presence of the daughter opened the cell and ate the daughter's egg, then she laid an egg and resealed the cell (n=9; Fig. 2). In 3 occasions the daughter laid an egg and left the nest, but after 114 seg (n=3) the mother opened the cell and replaced the daughter's egg with her own. Clearly, the mothers took more time (Mann-Whitney test, Z= 2.31, P= 0.18) to open and eat the daughters' eggs when both were in the nest (559±232 seconds, n=9) than when she was on her own (114±56 seconds, n=3). In 6 occasions the mother laid an egg before her daughter, this occurred when the cell was almost fully provisioned and the daughter was foraging. In two out of these six occasions, the daughter, after returning from her foraging trip, reopened the cell and ate the mother's egg. After this, the mother in the presence of her daughter opened the cell again and ate the daughter's egg and laid a second egg of her own. In two occasions, the daughter did not open the cell and started searching for another cell to discharge her food load. In all the occasions when the mother opened cells and ate the eggs, there was no physical opposition by the daughters (n=17). However, when the daughter tried to open a cell, the mother approached her daughter and displayed a threatening behavior with her front legs and mandibles open but without any physical contact with her. In the 19 ovipositions that were observed in MFN1, 18 cells ended with eggs laid by the mother (94.7 %), indicating a reproductive dominance by the founder female.

In the MFN2 nest, the mother remained in the nest most of the time. In only one occasion the mother left the nest (for 35 min) but when returned from outside, she reopened the cell where she previously had laid an egg, ate it and laid another one. As observed in the MFN1 nests, the mother in presence of both daughters opened the cells, ate their eggs, laid hers and resealed the cells. The mother helped her daughters to elongate the cells while they were not in the nest and remained at the nest entrance assuming a guarding activity while the daughters were outside foraging. In the MFN2 nests, there was a reproductive dominance by the mother too. But interestingly, the number of cells oviposited by the mother were only 9 (out of 20 observed ovipositions: 45.1 % compared with 94.7 % in MFN1) and the rest were shared by the 2 daughters (30 % and 25 % respectively) which resulted in half of the brood produced by the mother in MFN1 but still representing a higher reproductive rate than that of her offspring.

The presence of parasites of the genus *Anthrax* spp. (Family Bombyliidae) and *Hoplostelis bivittata* (Megachilidae, Anthidiini) was observed only in SFN nests. This is the first register of both parasites in Euglossine nests in the Yucatan Peninsula. The parasites entered the nest when the female was foraging outside. In the case of *H. bivittata*, after entering the nest, the female parasite closed the entrance using the resin left by the bee and immediately after, opened a cell to remove the *E. viridissima* larva, laid her egg on top of the food and resealed the cell, and then she opened the entrance and left the nest. Seventeen of the 98 cells studied (17 %) had an *Anthrax* fly and one a *Hoplostelis bivittata* (1 %). It is important to underline that not a single cell had parasites in multiple females nests (Chi-square= 11.91 df= 1, P= 0.006).

## Discussion

Our data on *E. viridissima* give evidence for the existence of the basic prerequisites of sociality in this species (Michener and Brothers 1974). Observations in MFN showed that generational overlap occurred in this species and that daughters helped their mothers in reactivating some of their nests. Reactivation in MFN involved physical tolerance (lack of aggression) between females but most important that during this phase a reproductive division of labour was produced, the mother remaining as the nest guard (and predominantly reproductive female) and the daughters actively engaging in food collection. All daughters participating in nest reactivation foraged and provisioned their own cells, a similar behavior to that observed in *E. intersecta* (Zucchi et al., 1969), *El. nigrita* (Santos and Garófalo, 1994) and recently in *E. townsendi* (Augusto and Garófalo, 2004).

Interestingly, our results in *E. viridissima* show that nest reactivation by multiple females was performed by genetically related individuals and always in matrifilial association (not sororal nests were found) which contrast with findings in other *Euglossa.* However, more nests, especially with more than two females would be needed to corroborate if this is the rule in *E. viridissima.*

There were no differences during the process of cell construction, foraging and provisioning in SFN and MFN which reveals that advantages for social nesting may not be linked with the time involved in cell construction, this is further supported by the similar rates of cell production per female in SFN and MFN. However, multiple female association may find an advantage in the exploitation of food resources since in these nests the diversity of plants visited can be significantly higher compared to that in solitary females (Ramírez-Arriaga and Martínez-Hernández, 1998)

In MFN, all females were presumably mated but the daughter(s) acted as foragers/egg-laying females (=FELF) meanwhile the mother acted as the egg/laying female (=ELF), a similar behaviour to that found in *E. townsendi* (Augusto and Garófalo, 2004). In *E. viridissima*, eggs laid by FELF in the cells previously provisioned by them, thus acted as trophic eggs considering that were eaten by the ELF. This is also supported by the fact that the mother didn't forage (except in few occasions) thus, apparently obtaining nutriments mainly through oophagy.

In *E. viridissima*, no aggressive behavior was observed by the mother towards her daughters when they laid an egg, similar to the findings in *E. townsendi* (Augusto and Garófalo, 2004). In contrast, in *E. cordata* (Augusto and Garófalo 1994) the mother or older daughters impose their dominance over reproduction showing antagonistic (aggressive) behavior towards other daughters (matrifilial association) or sister females (sororal association) which act as subordinated females. However, in *E. viridissima* the mother showed threatening behavior when the daughters tried to touch a cell with her egg, which may be considered physical domination.

Oophagy of some mother's eggs by her daughters was also observed in *E. viridissima*, however, the mother cannibalized such eggs and replaced them with her own, confirming her reproductive dominance. It was interesting to note that the mother may not have a mechanism to detect the origin of the brood, In the only occasion that the MFN2 mother left her nest cheating by her daughters was prevented by destroying eggs that may have been laid in her absence (even her own eggs), something not previously reported in other *Euglossa.* The behavior between the mother and her daughters in *E. viridissima* resembles that of a parasitic female that improves her own fitness on detriment of her daughters' reproduction (Subblefield and Charnov, 1986; Garófalo, 2006). This seems a primitive case of mother policing (coercion) on her daughters that may evolve as a result of the mother being twice as related to her offspring as to her daughter's offspring (grandoffspring) (Ratnieks and Wenseleers, 2007).

The oophagy of daughter's eggs preceding the oviposition of the mother was also observed in reactivated nests of *E. cordata* (Augusto and Garófalo, 1994) and *E. townsendi* (Augusto and Garófalo, 2004) but different to that found in other *Euglossa* species like in *E. hyacinthina* where only communal association was established between non-related females and reproductive division of labor doesn't occur (Soucy et al., 2003).

In *E. viridissima* the total number of cells built increased with the number of females as reported in *E. townsendi* (Augusto and Garófalo, 2004). However, the number of cells per female was similar between SFN and MFN. This difference is attributed to the fact that some females (in this case the mother) do not build cells (Michener, 1974). This apparent disadvantage may not be so when one considers that the invasion of cells by parasites in MFN is very low compared to cells from SFN, so the net gain per female may be much higher in MFN in the long run. Nevertheless, this gain may be higher for the mother through policing of her daughters and producing more offspring than on her own. This result is in contrast with what was reported in *E. townsendi*, where no advantage against parasites was evident in reactivated nests by two or more females during matrifilial or sororal association (Augusto and Garófalo, 2004).

Additional advantages for social nesting in Euglossines have been cited for both, the mother and her daughters. The mother may increase her survival (less risk for predation in the nest) and reproductive life and the daughters may take the dominant (reproductive) position when the mother dies as in *E. cordata* and *E. townsendi* (Augusto and Garófalo, 2004; Garófalo, 2006).

Our results in *E. viridissima* also indicate that social nesting seems to involve kin selection as a first factor selecting for tolerance and cooperation that is later enforced by some kind of coercion. The reproductive division of labour in this species occurred without apparent physical dominance of the mother on her daughters which is in agreement with kin selection. In this respect, kin selection theory predicts that reproductive competition in animal associations should be less strong in related individuals as we found in *E. viridissima* nests (Ratnieks and Wenseleers, 2007). Studies where related and unrelated females nest in association may help to explain our results. In *Xylocopa* (Antophoridae) multiple nesting females are non related and egg destruction by the foundress and the helper involves intensive and energy consuming interactions between both females (Stark et al., 1990; Hogendoorn and Velthuis, 1993). In contrast in *Lasioglossum* (Halictidae) where females are genetically related, the mother eats the daughters eggs and there is no opposition on behalf of the latter (Michener and Brothers, 1974) as we found in *E. viridissima.* Thus, *E. viridissima* seem to fit the hypothesis on kinship as a first step to explain reproductive division of labor in genetically related individuals. However, mother oophagy reveals that coercion on the daughters existed too as a mean of reinforcing such division of labor.

As to why daughters remained in their nest in spite of being coerced by her mother when nesting sites were not in shortage (potential nests were provided each month) is not clear. The advantages against parasites in MFN have been discussed before but other factors may also be involved. In *Lasioglossum,* Michener and Brothers (1974), suggested that some females remained in their original nest because they had less developed ovaries and were physiologically less fit. These females may gain more by helping to rear their mother's offspring than trying to survive alone, find (or fight for) a nest and reproducing at a comparatively lower rate (Michener and Brothers, 1974). Physiological differences (asymmetries) between related females in MFN have not been studied in Euglossines but it may be a step towards the evolution of a female caste (workers) in Apidae. In fact, variability in body size (attributed to mother response to food fluctuation) has been found in males of *El. nigrita* (Peruquetti, 2003). The potential existence of means of controlling the development of the female offspring by the mother is worth evaluating since such features can result from individual selection also acting on queens. This may be so since worker characteristics that permit control by the queen may be favored by selection for queens that produce controllable workers (Michener and Brothers, 1974).

In summary, the few studies on sociality in *Euglossa* have so far revealed that a wide range of social behaviors occur in this genus including, solitary, communal and with primitive reproductive division of labor, like in our study. Multiple factors involving food and nest availability to different levels of pressure imposed by parasites may favor such a diverse range of nesting behaviors. Interestingly, kin selection and coercion seem involved in the establishment of matrifilial nests as evident in our results. Molecular studies could shed light upon the social organization of *E. viridissima* and other species of Euglossines and on their phylogenetic relationships to establish the origins of sociality in Apidae.

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