Research article

Solitary and group nesting in the orchid bee *Euglossa hyacinthina* (Hymenoptera, Apidae)

S. L. Soucy [1,2], T. Giray [3,4] and D. W. Roubik [3]

[1] *Department of Ecology and Evolution, State University of New York, Stony Brook, NY 11794-5245, USA*

[2] *Current address: Department of Entomology, University of California, Davis, CA 95616, USA, e-mail: slslubell@ucdavis.edu*

[3] *Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002-0948, USA*

[4] *Current address: Department of Biology, University of Puerto Rico, PO Box 23360, San Juan, PR 00931, e-mail: tgiray2@yahoo.com*

Summary. Orchid bees (Euglossini) provide a potentially informative contrast for examining origins of advanced social behaviour in bees because they are the only tribe in the apine clade that do not form large colonies or have queens and workers. We investigated natural nests of *Euglossa hyacinthina* Dressler, an orchid bee that nests singly or in groups. By comparing the two types of nests, we examined if individuals in a group merely share the nest (are communal) or exhibit a level of social organization where there is reproductive division of labour among the females. Observations are consistent with communal nesting, indicating that all females in group nests are reproductively similar to the solitary nesting females because the provisioning of young, as well as the ovary development and mating status of females sharing nests were not different than that of solitary-nesting females. Also, multiple female nests did not produce a female-biased brood as predicted for nests with reproductive division of labour. We also investigated potential advantages of group nesting vs. individual nesting. We demonstrate that per capita offspring production is lower in nests with more than one female. However, we found that nests with single females were left unattended for longer periods of time during foraging, and that there was a high incidence of natural enemy attack in nests when females were absent. Group and solitary nesting may be advantageous under different conditions.

Key words: Nesting biology, social behaviour, social evolution, Euglossine bees.

Introduction

Explaining how a highly integrated social organization evolves from a solitary origin is crucial to our understanding of biological organization (Darwin, 1859; Seeley, 1995; Page, 1997). The corbiculate apid clade, which includes bumble bees (Bombini), honey bees (Apini), stingless bees (Meliponini), and orchid bees (Euglossini), is the only group of bees that exhibits highly eusocial behaviour (Michener, 1974). Such behaviour may have arisen multiple times within this clade but the issue is not resolved (see review in Lockhart and Cameron, 2001). While the study of highly social species is informative for understanding the maintenance of social behaviour, the study of closely related groups that express solitary or semi-social behaviour is necessary for investigating the origin of highly-social organization. Excluding parasitic species, orchid bees are the only members of the apine lineage that do not form large colonies with a queen and non-reproductive workers (Michener, 1974; Roubik, 1989). Therefore, they are a key group for studying precursors to highly social behaviour.

In this study we examined nesting behaviour, reproductive output, brood provisioning, and social interactions in natural nests of the orchid bee *Euglossa hyacinthina* Dressler (Apidae: Euglossini). The nests of *E. hyacinthina* are hollow constructs made entirely of resin, and populations of this species contain both solitary and multifemale nests (Eberhard, 1988; see also Young, 1985). This species is ideal for investigating issues pertaining to the origins of sociality because, unlike other Euglossini, many individual nests may be located. Moreover, most of what is known about euglossine sociality is based on studies involving highly modified habitats and small nest boxes of species that ordinarily nest in cavities (e.g., Roberts and Dodson, 1967; Zucchi et al., 1969; Garófalo, 1992; Santos and Garófalo, 1994; Ramírez-Arriaga et al., 1996). This paper describes euglossine behaviour in natural nests that occur in the open; the nesting behaviour of these bees under natural conditions has received little attention (but see Myers and Loveless, 1976 and Eberhard, 1988).

Eberhard (1988) provided basic natural history of the nesting biology of a Costa Rican population of *E. hyacinthi-*

na based on natural nests. Here, we present for the first time data on ovary development, mating status, brood sex ratio, and foraging observations in *E. hyacinthina*. The first goal of our research was to examine whether group-nesting individuals merely share a nest or demonstrate some level of reproductive division of labour. Both states occur in Euglossini (Michener, 1974). First we examined the number of cells provisioned and the number of adult females in a nest. Unless egg cannibalism or some other loss of eggs occurs (e.g., Kukuk, 1992), more females than provisioned cells indicates that some females are reproductively inactive. Next we examined ovary development and mating status of solitary-nesting and group-nesting females. Unmated individuals, individuals with reduced ovaries, or a higher variance in ovary development among group-living than solitary individuals could all suggest reproductive differentiation. Finally, we determined sex ratio as an indicator of social organization. Sex-ratio theory predicts that broods will be female-biased in a social population composed of nests with multiple related females, some of which are non-reproductive, although such nests may be male biased during certain seasons when reproductives are produced. Female bias is also predicted for populations experiencing inbreeding. In populations exhibiting other types of sociality, when queens control offspring sex ratios, and in orphaned nests, a female bias is not predicted (Hamilton, 1967; Trivers and Hare, 1976; Boomsma, 1991).

The second goal of our research was to compare per capita productivity of solitary-nesting and group-nesting females to understand reproductive costs or benefits of these behaviours in the same population. For instance, multi-female nests may be profitable because they result in increased per capita reproductive output due to local fitness enhancement (e.g., Packer, 1993; Bull and Schwarz, 1996; Cronin and Schwarz, 1997; Tierney et al., 1997). Additionally, costs associated with solitary nesting also may favor group nesting. For instance, the need for shared nest defence (Lin and Michener, 1972; Alexander, 1974; Abrams and Eickwort, 1981), limited nest site availability (McCorquodale, 1989; Banschbach and Herbers, 1996) and costly nest construction (Eickwort, 1981; McCorquodale, 1988; Strassmann et al., 1988) all favor nest cohabitation because females who nest together may realize increased fitness. We investigated the first of these as a factor promoting group-nesting behaviour.

Materials and methods

We conducted this study in a cloud forest at 1400 m above sea level near Fortuna, Panama, in Chiriqui Province. Individual females of *E. hyacinthina* build hollow aerial nests made of resin, attached to thin, upright stems of shrubs (see Fig. 3 in Eberhard, 1988). We located a total of 79 nests from 29 November 1996 to 18 February 1997 in five different censuses and in repeated searches at approximately two-week intervals. We searched for nests along a 29 km section of the highway between the towns of Los Planes and Chiriqui Grande, by scanning the secondary vegetation along the roadside and the banks of nearby streams. We recorded the number of brood cells and adult females within each nest. Nest contents were checked regularly during the study period at different times of day in order to more accurately assess the num-

ber of resident adult females. This provided us with a count of the minimum number of female inhabitants. Because our observations were consistent and extensive, we feel that these are accurate measures of female inhabitants. We could record only location information on 27 of the 79 nests because of inaccessible locations or because their entrances were sealed.

We calculated the average per capita productivity in single- and multi-female nests. We considered the number of cells in a nest, and the number of developing brood in sealed cells, and divided by the number of adult female inhabitants.

In order to obtain more specific information on adult females, developing brood, and the presence of predators and parasites, we collected 31 nests in February 1997. We cut the stem of the plant to which each nest was attached approximately 15 cm below the bottom of the nest, and immediately placed the nest in a cooler of ice for transport. Sealed nests (nesting females make a resin curtain across the nest entrance at night and during inclement weather) were collected in this way and brought to the field station where we transferred them to a 4 °C refrigerator for approximately two hours.

We opened each resin nest by cutting a broad circular opening with a hot razor blade and removing the front panel of the nest (Fig. 1A). Any adults in the nest were marked with a numbered plastic tag (Opalithplättchen, produced by Chr. Graze, Endersbach, Germany) glued to the thorax. We opened each brood cell with a hot razor blade and removed the contents. Pre-emergence adults with fully sclerotized bodies found in sealed cells were also marked with numbered plastic tags. For each nest dissection, we recorded the number of adults, the number, condition, and contents of cells, the presence and type of parasites and predators, and evidence for nest reuse (described in the Results section).

We observed the activities of bees in natural nests for a total of 27 observation sessions on 18 days, for a total of 3580 minutes (1608 minutes observing single-female nests and 1972 minutes observing multi-female nests). Our observations involved 40 different bees (20 from single-female nests and 20 from seven multifemale nests). Observations at nests usually began between 0800 and 0900 hours from 30 November 1996 through 20 February 1997. We observed nests for 30 minutes and would either remain for additional observations if bees in the nest were active, or move to another nest if we saw no activity. We observed the activities at different nests each day so that we might avoid pseudoreplication. During observation sessions, we timed individual foraging trips and recorded whether the forager carried pollen, resin, or nothing on her corbicula (presumably carrying nectar) upon her return. We computed the percentage of time individual bees spent foraging for provisions (pollen and nectar) while the nest entrance was open.

We examined the mating status and ovary development of adult females in single and multifemale nests. We dissected the abdomens of a total of 23 adult females from seven single-female nests and seven
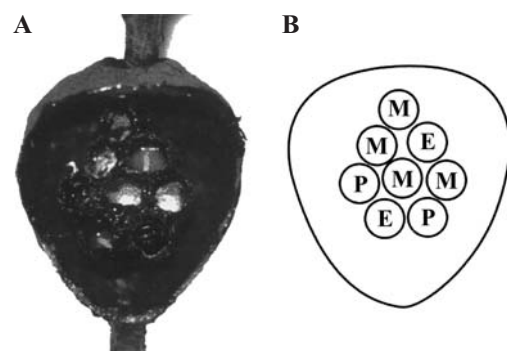
Figure 1. A. The outer envelope of a nest inhabited by two adult females has been opened to reveal eight brood cells and their contents. B. Diagram indicating the contents of the nest in A. Four of the brood cells are empty except for fecal meconia (M), indicating prior emergence of adults. Two cells contain pigmented pupae (P) and two others contain eggs on fresh provisions (E).

multi-female nests (five nests of two females, and one nest each of three females and four females). We measured the total length of developed terminal oocytes (four on each side) for each female and divided this number by eight to calculate the mean length of developed terminal oocytes per female. We sqashed the spermathecae on glass microscope slides and examined them under a light microscope (at 40 ×; e.g. Wcislo et al., 1992).

We calculated the sex ratio of the brood of 25 nests for which we had complete sex ratio information. We determined the sex of pupae and emerging adults by their morphological characteristics (antennal segments, 13 in males, 12 in females; corbiculae, present in females, absent in males; and a tuft of hair on the thorax, present in males, absent in females).

We obtained several measures of the quality of nest protection in single and multifemale nests. 1.) During nest dissections we recorded the incidence and type of brood mortality. 2.) We observed nest maintenance by peering through the nest entrance hole while adults were inside. 3.) To determine the percentage of time a nest was accessible yet unoccupied, we calculated a time budget for females when the nest entrance was opened.

Results

Thirty-five of the 52 nests examined were inhabited by one or more adult females (1.6 ± 0.2 females per nest, range $1-5$), the remainder contained no adults. The mean number of cells in a nest was 5.8 ± 3.1 with a range of 1 to 15 cells. Females construct brood cells in a cluster inside the nest envelope, so that the first cells are attached to the stem and additional cells are built outward upon preexisting cells (Fig. 1; see also Eberhard, 1988). This was deduced from the stages of developing offspring in the brood cells, and by observing the pattern of cell construction in nests observed since initial construction.

Twenty-four nests were inhabited by a single female and 11 others contained two or more females (Fig. 2). Brood cells near the stem containing fresh provisions, surrounded by cells with late instars or pupae, indicate prior emergence and reuse of the empty cells (Fig. 1 B). A minimum of 18 of 52 nests showed evidence of reuse. These include 10 of 11 mul-
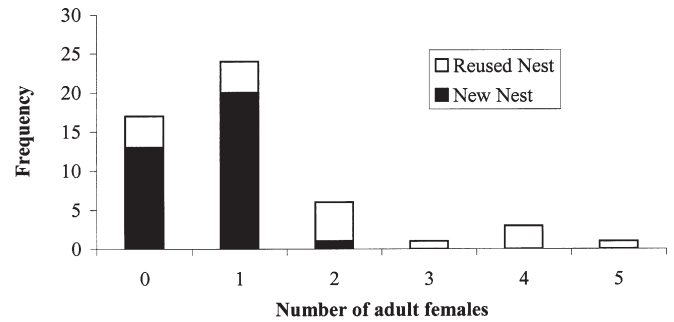
Figure 2. Nests were occupied by zero to five adult females. All but one of the multifemale nests showed evidence of reuse ($N = 11$) while 83% of single female nests were new constructions ($N = 24$).

tifemale nests, four single-female nests, and four additional nests that contained no adult females. Reused nests contained 7.8 ± 2.4 cells (range 5 to 15). The total per capita number of cells (t-test: $t_{[0.05, 33]} = 0.92$, NS) and the per capita number of developing brood (t-test: $t_{[0.05, 33]} = 2.3$, NS) was not different between new and reused nests that contained adult female inhabitants (Table 1). Multifemale nests were more likely to show signs of reuse than were nests inhabited by a single female (G-test of independence with William's correction: $G_{adj[0.05,1]} = 17.5$, $P < 0.001$).

There were significantly fewer cells per female in multifemale nests (2.8 ± 1.1, $N = 11$) than in single-female nests (4.9 ± 3.1, $N = 24$) (t-test: $t_{[0.05, 33]} = 4.2$, $P < 0.005$). In some cases of nest reuse, the total number of cells in a nest does not reflect the productivity of the current inhabitants because they only have reused some of the cells. Therefore we also calculated the number of cells that contained developing brood. There were fewer cells per capita containing developing brood in multifemale (1.5 ± 0.8, $N = 11$) compared to single-female nests (2.5 ± 1.5, $N = 24$; t-test: $t_{[0.05, 33]} = 2.5$, $P = 0.005$). By both measures, females in multifemale nests had lower reproductive output than females who lived alone.

Table 1. The occupants and contents of the nests examined in this study.

Type of nest	N	Average number of cells in nest	Average number of cells containing brood	Average number of provisioned cells**
All	52	5.8 ± 3.0	3.8 ± 2.6	0.8 ± 0.9
Unoccupied	17	5.9 ± 2.5	4.8 ± 2.9	0.2 ± 0.5
Occupied	35	5.7 ± 3.3	3.3 ± 2.3	1.1 ± 0.9
Single-female	24	4.9 ± 3.1	3.0 ± 2.3	0.7 ± 0.4
Multi-female	11	7.6 ± 3.1	4.0 ± 2.2	1.7 ± 1.3
New construction	34	4.7 ± 2.6	4.0 ± 2.7	0.4 ± 0.5
Single-female	20	3.9 ± 2.1	3.1 ± 2.1	0.7 ± 0.5
Multi-female	1	2	2	0
Unoccupied	13	6.0 ± 2.7	5.5 ± 2.9	0.0 ± 0.0
Reused*	18	7.8 ± 2.4	3.3 ± 2.4	1.4 ± 1.1
Single-female	4	9.5 ± 3.1	2.3 ± 3.2	1.0 ± 0.0
Multi-female	10	8.2 ± 2.6	4.2 ± 2.2	1.9 ± 1.2
Unoccupied	4	5.7 ± 2.1	2.3 ± 1.3	0.8 ± 0.9

* Reuse of nests was determined by evidence as described in the text.
** Provisioned cells are open cells containing fresh provisions and no egg.
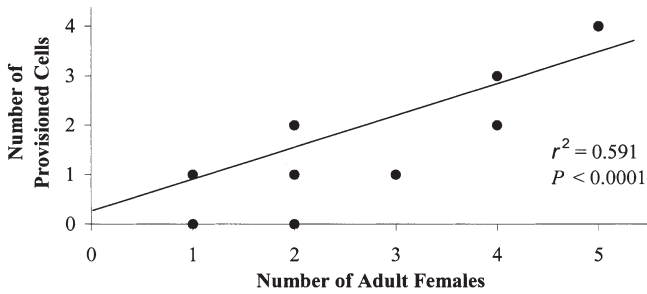
Figure 3. The reproductive output of nests increases with greater numbers of resident females. The number of brood cells being actively built or provisioned is correlated with the number of adult female inhabitants.

Figure 4. Five of 10 nests inhabited by multiple females are more female biased than predicted for a 1:1 sex ratio, yet the overall sex ratio in multifemale nests is not different from 1:1 using binomial probabilities. Nine of 13 nests inhabited by single females have more females than predicted for a 1:1 sex ratio.
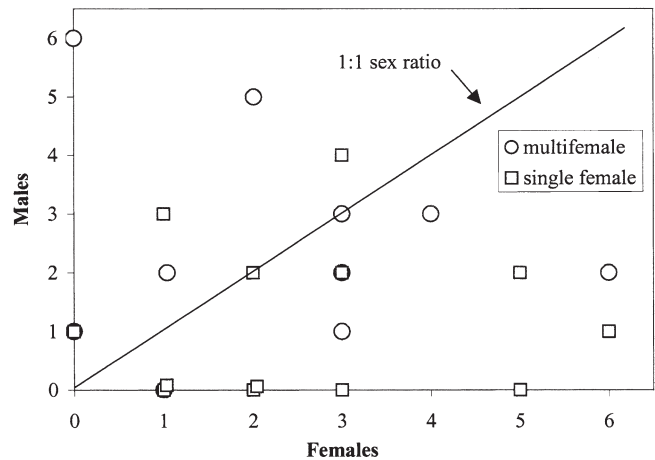
Behavioural observations indicate that most or all females in a group nest may be reproductively active. Across all nests we found a positive correlation between the number of adult females and the number of open cells containing fresh pollen provisions ($r^2 = 0.59$, $N = 35$, $P < 0.0001$; Fig. 3). However, the slope of this relationship was significantly less than one ($r = 0.77$ not different than $r = 1$, $P < 0.05$, $t = 2.1$, df = 33) and did not intersect the origin.

Physiological correlates also indicate that all females in a group nest may be reproductively active. Group and solitary nesting females had similar ovary development and all except one individual were mated. This female had recently emerged (she was indigo in color) into a nest with one other adult female. Two females that we found as pre-emergence adults on 5 February 1997 were both mated and contained bulges in their ovarioles about 50% of the size of a fully-developed egg by 21 February 1997 (by 16 days old). From these observations we infer that mating and ovary development occur within 16 days after emergence.

The mean length of developed terminal oocytes for group-nesting females (1.2 ± 0.1, $N = 16$ females from 7 nests) was not significantly different from solitary-nesting females (1.1 ± 0.1, $N = 7$ females from 7 nests, t-test: $t_{[0.05, 21]} = 0.36$, NS). Variance in the length of developed terminal oocytes of group-nesting females was not different from that of solitary-nesting females (F_{max}-test: $F_{max\ 0.05\ [2,6]} = 1.0$, NS). There was no evidence for egg resorption (yellow bodies) in the ovaries of any females.

In *E. hyacinthina*, sex ratios were compatible with all females being reproductively active in group-nests. There were 58 females among 101 sexed brood from 25 nests (nests were inhabited by zero, one, or more than one adult females). This ratio is not significantly different from 1:1 using binomial probabilities ($X^2_{0.05[1]} = 2.28$, NS). Multi-female nests produced a sex ratio of 23:25 (47.9% female) whereas the sex ratio in single female nests was 35:18 (66.0% female). Multiple female nests did not produce a brood that was significantly more female biased than single female nests ($X^2_{0.05[1]} = 3.3$, $0.1 < P < 0.05$; Fig. 4).

It may be argued that the dry weights of males and females, not the number of males and females as we report, is the best measure of an egg-layer's investment in offspring (Danfort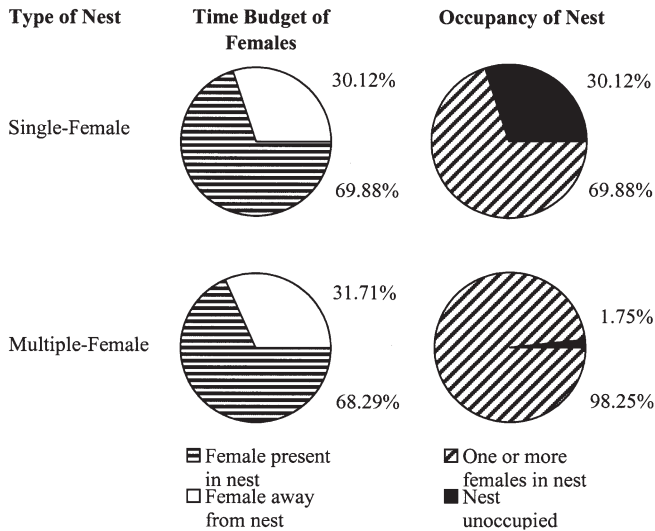h, 1990), because the resource investment in a female is greater than in a male for many bee species (e.g. Mueller, 1991; Boomsma and Eickwort, 1993; Packer and Owen, 1994). However, the head widths of males and females of *E. hyacinthina* are not significantly different (mean male headwidth = 4.32 mm ± .04, $N = 9$, mean female headwidth = 4.39 mm ± .03, $N = 12$, t-test: $t_{[0.05, 19]} = -1.40$, NS).

For individual bees, the mean time each female spent away from the nest was not different between solitary and group nests (Fig. 5). Females that nested alone ($N = 20$) spent 24.8% of their time on trips from which they returned with pollen and nectar, 5.7% on trips from which they returned with resin. Females that inhabited multifemale nests ($N = 20$) spent 23.8% of their time on trips from which they returned with pollen and nectar, 0.5% on trips from which they returned with resin (we were unable to determine the objective of 7.3% of the trips). The variance in percent of time spent on foraging trips among group-living females was not different from that for solitary females (percent time spent on foraging trips by solitary females = 30.5 ± 31.1; percent time spent on foraging trips by group-living females = 27.7 ± 28.8; F_{max}-test: F_{max} 0.05 [2,19] = 2.8, NS).

Multi-female nests were inhabited a greater portion of the time than were single-female nests, while the nest entrance was open ($N = 20$ for solitary nests, $N = 7$ for multifemale nests). Solitary nesting females spent 69.9% of their time in the nest, leaving the nest unoccupied 30.1% of the time. With the nest entrance opened, individual females inhabiting multifemale nests spent an average of 68.3% of their time in the nest, but because their foraging flights were staggered, multifemale nests were unoccupied only 1.7% of the time (Fig. 5).

There was substantial parasitism and predation of *E. hyacinthina* in the study population. Ten of the 31 dissected nests had some type of natural enemy including mould, ants, spiders, earwigs, lepidopterans, mutillid and encyrtid wasps,

Type of Nest	Time Budget of Females	Occupancy of Nest

Single-Female — 30.12% / 69.88% (Time Budget); 30.12% / 69.88% (Occupancy)

Multiple-Female — 31.71% / 68.29% (Time Budget); 1.75% / 98.25% (Occupancy)

⊟ Female present in nest
☐ Female away from nest

☑ One or more females in nest
■ Nest unoccupied

Figure 5. While the nest entrance is open, females who nest alone spend approximately 30% of the day away from the nest ($N = 20$). Although the time allocated to tasks away from the nest is similar for individual females in multiple-female nests, the presence of additional inhabitants results in the nest being left unattended less than 2% of the day ($N = 20$). These are summary (not average) values for all females inhabiting each type of nest.

and the cleptoparasite *Hoplostelis* (Family Megachilidae). All of these nests were uninhabited by adult females of *E. hyacinthina*. In three other uninhabited nests, as well as all of the 19 nests inhabited by one or more adult females of *E. hyacinthina*, we never observed a natural enemy (presence of natural enemies in inhabited vs. uninhabited nests; *G*-test of independence: $G_{adj [0.5, 1]} = 20.0$, $P < 0.0001$).

Discussion

Multiple lines of evidence indicate that in *Euglossa hyacinthina* all females, including those in group-nests, are reproductively active. The high incidence of nest reuse leads us to infer that multifemale nests usually result from the reuse of nests by daughters after their emergence. This species demonstrates some of the characteristics exhibited by social bees such as haplodiploidy, overlap of generations, and nest cohabitation, but *E. hyacinthina* seems primarily solitary or communal. Our results indicate that there is a trade-off between solitary and group nesting, an observation on bee nesting biology made by Michener (1964) nearly three decades ago. Females in multiple-female nests experience lower reproductive output (43% fewer cells per capita, and 40% fewer developing brood per capita), yet the presence of adults may reduce the incidence of attack by natural enemies. This strategy appears to be a form of "bet-hedging" – accepting slightly lower average fitness in exchange for a lower variance in success (Seger and Brockmann, 1987).

We found that a substantial proportion of nests are inhabited by more than one female. This is consistent with the

observations of Eberhard (1988) who reported 2.1 ± 1.2 *E. hyacinthina* females per nest (range 1–5). We hypothesize that nests may be shared by females of the same generation (sister-sister), of different generations (mother-daughter), or perhaps on rare occasions by unrelated individuals. We specifically observed the inheritance of a nest by a female born into the nest on several occasions by marking pre-emergence adults and observing that they remained in the nest to produce their own offspring. Observations of the movement of tagged individuals and analysis of genetic markers will reinforce our observations.

In *E. hyacinthina,* there probably is an upper limit to the number of adults who can occupy a nest, because the outer envelope cannot be expanded to accommodate ever-larger cell clusters. It is interesting to note that the outer envelope is also restrictive to nest growth in some wasp species (e.g. *Protopolybia* sp.) but not in others (e.g. the genera allied to *Parachartergus*; Wenzel, 1991). Both *Protopolybia* and *Parachartergus* wasps are eusocial, so while the size of the outer envelope may restrict the number of inhabitants in a nest, it may not restrict the expression of eusocial behaviour.

The *E. hyacinthina* multifemale nests appear to be communal. The number of provisioned cells in nests with varying number of females supports the conclusion that all females in a nest are potentially reproductive. One may conclude that one female in multiple-female nest may exhibit reproductive dominance over her nestmates, and that this individual may have higher reproductive output when foraging is aided by subordinates. However, foraging data is in conflict with this explanation; all bees in group-nests appear to forage for provisions and at rates similar to solitary females.

The ovary development and mating status data also suggest communal social structure. Females that share nests have comparable levels of ovarian development, which are similar to solitary females. If egg-laying in multiple-female nests was dominated by only one female we would expect a large variance in ovary development because the egg-layer would have a series of developing oocytes while the subordinates would have few or none. Our observations still are not conclusive because it is possible that egg-cannibalism and cell usurpation occur, as known for other bee species including euglossines (Michener and Brothers, 1974; Garófalo, 1985; Robinson et al., 1990; Kukuk, 1992; Ward and Kukuk, 1998), in which case a dominance hierarchy among females may exist.

Finally, population and group nest sex ratios are 1:1 and compatible with communal nesting rather than reproductive division of labour. This sex ratio also indicates that inbreeding is not occurring in this species. Taken together, the potential conflicts between the alternative interpretations of these lines of evidence, and the single direction of total evidence, makes communal organization the most likely explanation for group nesting in this population of *E. hyacinthina*.

Interestingly, although females appear to be acting individually, there does seem to be some form of communication among nestmates in multiple-female nests. Based on our repeated observations of nest inhabitants, some of which

were tagged, we found that females seal the nest at night and in bad weather only after all inhabitants have returned to the nest. This may demonstrates that individuals are aware of the presence of their coinhabitants (although there may be some biological clock at work). This observation is in contrast to the behaviour of another bee species. In the halictine bee *Lasioglossum* (*Evylaeus*) *villosulus*, which is generally solitary with occasional multifemale nests, females do not wait for nestmates to return before closing the nest entrance (Plateaux-Quénu et al., 1989). There also is a noticeable lack of aggression among nestmates in *E. hyacinthina*. Tolerance of nestmates has been indicated as a prerequisite (either as a preadaptation or as an appropriate "flexible response") for group-living behaviour (West-Eberhard, 1987).

It is notable that there are multiple lines of evidence for communal behaviour in *E. hyacinthina*. The results of the present study in combination with previous work, suggest that euglossines demonstrate a range of nesting strategies, including solitary, communal and eusocial behaviours. A phylogeny of the genus may reveal that there have been several origins or reversals of social behaviour, a phenomenon documented for other groups of bees (Wcislo and Danforth, 1997). Clearly there is a need for more information on the social organization of other euglossines, and on the phylogenetic relationships.

We found that group-nesting females have lower per capita reproductive output than solitary females, a paradox noted by Michener (1964) for many hymenopterans. In *E. hyacinthina*, this simply may reflect the fact that multiple-female nests contain as yet reproductively immature females, whereas the majority of solitary nests are original nests constructed by reproductively mature individuals. It also should be noted that the calculation of reproductive output did not include failed nests. Whether a higher rate of nest failure applies to single- or multiple-female nests in nature, an important facet determining the selective value of single-versus multiple-female nests, is unknown. Also, the estimates of reproductive output in both single and multifemale nests are most likely overestimates because we counted the number of sealed cells as a measure of reproductive output. This measure could be inflated due to subsequent loss of offspring before emergence as an adult, and due to the death of reproductive adult females before the emergence of her offspring. This problem should not, however, introduce a systematic bias into the results; the same phenomena would apply to both single and multifemale nests. Thus, we argue that multifemale nests do experience lower per capita output, and females who share a nest tolerate lower output because they gain some other benefit by sharing a nest.

One benefit of shared nests may be increased vigilance against predators and parasites (Lin and Michener, 1972; Alexander, 1974; Abrams and Eickwort, 1981). For *E. hyacinthina*, nests of solitary females are unattended for a greater portion of each day than are nests with multiple-females. Because *E. hyacinthina* is a mass-provisioning species, the presence of an adult female should not affect the development of the offspring. However, we found that uninhabited nests are more likely to fall victim to natural enemies,

suggesting that adult females do play a role in protecting their offspring from attack by opportunistic species. Even if parasites and predators only move into a nest after a female dies, the presence of multiple-female nests may be a case of what Gadagkar (1990) calls "the advantage of assured fitness returns". If one of the females who shares a nest dies before her brood has fully developed, she may benefit from the presence of other females if they prevent the nest from being invaded following her death.

The negative relationship between occupancy and the presence of natural enemies is true for other hymenopteran species. In the primitively social wasp *Auplopus semialatus* Dreisbach, Wcislo et al. (1988) found that during 42 hours of observation a multifemale nest was unattended for less than one minute, and during that brief time a cleptoparasitic wasp entered a provisioned cell and probably laid an egg. In a solitary population of the sweat bee *Halictus rubicundus* Christ, nests in which the adult female died before her offspring emerged had 68% higher brood mortality than did nests that retained their foundress (Eickwort et al., 1996).

It is possible that the conditions favoring solitary and group nesting may fluctuate seasonally and with nest ontogeny. For instance, with seasonal fluctuations, an increase in predators and decrease in resin resources both may favor group-nesting behaviour. Under different conditions, solitary behaviour may predominate. Sex ratios in single and multifemale nests may also fluctuate seasonally. It is our observation that even though the variation in weather patterns throughout the year is slight in most years, there are definite patterns of flowering for important plant species (e. g., *Clusia* species as a source of resin). El Niño weather patterns may also cause significant changes in the flowering patterns of important plants (D. Roubik, pers. obs.) and could affect longer-term patterns in nesting behavior.

It is possible that group and solitary nesting are also stages in nest ontogeny. It may be that an individual female constructs a nest and, upon her death, all of her adult daughters inherit the nest. As they mature, the adult daughters may leave their natal nest to construct new nests (or in rare cases join existing nests elsewhere), and one may remain to be the sole inhabitant of their mother's nest. Our results do not preclude the possibility that the presence of single and multifemale nests in the same population is due to a combination of seasonality and nest ontogeny.

Our study highlights several areas of research that would provide important information on the social organization of *E. hyacinthina*. First, genetic analysis of adults and offspring will potentially provide information on the movement of individuals within a population, and the relationships among adults and/or immature offspring in a nest (e. g., Peters et al., 1999). Second, long-term observations of nest clusters and manipulative experiments (i. e., altering number of inhabitants of nests) may further elaborate the dynamics of nest reuse versus de novo construction, and the conditions that favor each. This study adds to the ever-increasing body of research that may provide valuable insight into the characteristics that facilitate or hamper the evolution of sociality in euglossine bees.

Acknowledgments

References

Abrams, J. and G.C. Eickwort, 1981. Nest switching and guarding by the communal sweat bee *Agapostemon virescens* (Hymenoptera, Halictidae). *Insect. Soc. 28*: 105–116.

Alexander, R.D., 1974. The evolution of social behavior. *Annu. Rev. Ecol. Syst. 5:* 325–383.

Banschbach, V.S. and J.M. Herbers, 1996. Complex colony structure in social insects: I. Ecological determinants and genetic consequences. *Evolution 50:* 285–297.

Boomsma, J.J., 1991. Adaptive colony sex ratios in primitively eusocial bees. *Trends Ecol. Evol. 6:* 92–95.

Boomsma, J.J. and G.C. Eickwort, 1993. Colony structure, provisioning and sex allocation in the sweat bee *Halictus ligatus* (Hymenoptera: Halictidae). *Biol. J. Linn. Soc. 48*: 355–377.

Bull, N.J. and M.P. Schwarz, 1996. The habitat saturation hypothesis and sociality in an allodapine bee: Cooperative nesting is not "making the best of a bad situation". *Behav. Ecol. Sociobiol. 39*: 267–274.

Cronin, A.L. and M.P. Schwarz, 1997. Sex ratios, local fitness enhancement and eusociality in the allodapine bee *Exoneura richardsoni*. *Evol. Ecol. 11*: 567–577.

Danforth, B.N., 1990. Provisioning behavior and the estimation of investment rations in a solitary bee, *Calliopsis* (*Hypomacrotera*) *persimilis* (Cockerell) (Hymenoptera: Andrenidae). *Behav. Ecol. Sociobiol. 27*: 159–168.

Darwin, C., 1859. *The Origin of Species by Means of Natural Selection*. John Murray, London. 513 pp.

Eberhard, W.G., 1988. Group nesting in two species of *Euglossa* bees (Hymenoptera: Apidae). *J. Kansas Entomol. Soc. 61*: 406–411.

Eickwort, G.C., 1981. Presocial insects. In: *Social Insects* (H.R. Hermann, Ed.), Academic Press, New York. pp. 199–280.

Eickwort, G.C., J.M. Eickwort, J. Gordon and M.A. Eickwort, 1996. Solitary behavior in a high-altitude population of the social sweat bee *Halictus rubicundus* (Hymenoptera: Halictidae). *Behav. Ecol. Sociobiol. 38*: 227–233.

Gadagkar, R., 1990. Evolution of eusociality: the advantage of assured fitness returns. *Phil. Trans. Royal Soc. London, Ser. B. 329*: 17–25.

Garófalo, C.A., 1985. Social structure of *Euglossa cordata* nests (Hymenoptera: Apidae: Euglossini). *Entomol. Gen. 11*: 77–83.

Garófalo, C.A., 1992. Comportamento de nidificação e estrutura de ninhos de *Euglossa cordata* (Hymenoptera: Apidae: Euglossini). *Rev. Bras. Biol. 52*: 187–198.

Hamilton, W.D., 1967. Extraordinary sex ratios. *Science 156*: 477–488.

Kukuk, P.F., 1992. Cannibalism in social bees. In: *Cannibalism: Ecology and Evolution Among Diverse Taxa* (M.A. Elgar and B.J. Crespi, Eds.), Oxford University Press, Oxford. pp. 214–237.

Lin, N. and C.D. Michener, 1972. Evolution and selection in social insects. *Quart. Rev. Biol. 47*: 131–159.

Lockhart, P.J. and S.A. Cameron, 2001. Trees for bees. *Trends Ecol. Evol. 16*: 84–88.

McCorquodale, D.B., 1988. Why do solitary wasps share nests? *Proc. Entomol. Soc. Ontario 119*: 93–94.

McCorquodale, D.B., 1989. Soil softness, nest initiation, and nest sharing in the wasp *Cerceris antipodes* (Hymenoptera: Sphecidae). *Ecol. Entomol. 14*: 191–196.

Michener, C.D., 1964. Reproductive efficiency in relation to colony size in hymenopterous societies. *Insect. Soc. 11*: 317–342.

Michener, C.D., 1974. *The Social Behavior of the Bees*. Belknap Press of Harvard University Press, Cambridge, MA. 404 pp.

Michener, C.D. and D.J. Brothers, 1974. Were workers of eusocial Hymenoptera initially altruistic or oppressed? *Proc. Nat. Acad. Sci. USA 71*: 671–674.

Mueller, U.L., 1991 Haplodiploidy and the evolution of facultative sex ratios in a primitively eusocial bee. *Science 254*: 442–444.

Myers, J.H. and M.D. Loveless, 1976. Nesting aggregations of the euglossine bee *Euplusia surinamensis* (Hymenoptera: Apidae): Individual interactions and the advantage of living together. *Canadian Entomol. 108*: 1–6.

Packer, L., 1993. Multiple-foundress associations in sweat bees. In: *Queen Number and Sociality in Insects* (L. Keller, Ed.), Oxford University Press, Oxford. pp. 215–231.

Packer, L. and R.E. Owen., 1994. Relatedness and sex ratio in a primitively eusocial bee. *Behav. Ecol. Sociobiol. 34*: 1–10.

Page, R.E., Jr., 1997. The evolution of insect societies. *Endeavor*, *21*: 114–120.

Peters, J. M., D.C. Queller, V.L. Imperatriz-Fonseca, D.W. Roubik and J.E. Strassmann, 1999. Mate number, kin selection and social conflicts in stingless bees and honeybees. *Proc. R. Soc. London, Ser. B 266*: 379–384.

Plateaux-Quénu, C., L. Plateaux and L. Packer, 1989. Biological notes on *Evylaeus villosulus* (K.) (Hymenoptera: Halictidae), a bivoltine, largely solitary halictine bee. *Insect. Soc. 36*: 245–263.

Ramírez-Arriaga, E., J.I. Cuaqdriello Aguilar and E. Martinez Hernandez, 1996. Nest structure and parasite of *Euglossa atroveneta* Dressler (Apidae: Bombinae: Euglossini) at Union Juarez, Chiapas, Mexico. *J. Kansas Entomol. Soc. 69*: 144–152.

Roberts, R.B. and C.H. Dodson, 1967. Nesting biology of two communal bees, *Euglossa imperialis* and *Euglossa ignita* (Hymenoptera: Apidae), including description of larvae. *Ann. Entomol. Soc. Am. 60*: 1007–1014.

Robinson, G.E., R.E. Page and M.K. Fondrk, 1990. Intracolonial behavioral variation in worker oviposition, oophagy, and larval care in queenless honey-bee colonies. *Behav. Ecol. Sociobiol. 26*: 315–323.

Roubik, D.W., 1989. *Ecology and Natural History of Tropical Bees*. Cambridge University Press, Cambridge. 528 pp.

Santos, M.L. and C.A. Garófalo, 1994. Nesting biology and nest re-use of *Eulaema nigrita* (Hymenoptera: Apidae, Euglossini). *Insect. Soc. 41*: 99–110.

Seeley, T.D., 1995. *The Wisdom of the Hive: The Social Physiology of Honey Bee Colonies*. Harvard University Press, Cambridge, MA. 384 pp.

Seger, J. and H.J. Brockmann, 1987. What is bet-hedging? In: *Oxford Surveys in Evolutionary Biology* (P.H. Harvey and L. Partridge, Eds.), Oxford University Press, Oxford. pp. 182–211.

Strassmann, J.E., D.C. Queller and C.R. Hughes, 1988. Predation and the evolution of sociality in the paper wasp *Polistes bellicosus*. *Ecology 69*: 1497–1505.

Tierney, S.M., M.P. Schwarz and M. Adams, 1997. Social behaviour in an Australian allodapine bee *Exoneura (Brevineura) xanthoclypeata* (Hymenoptera: Apidae). *Austr. J. Zool. 45*: 385–398.

Trivers, R.L. and H. Hare, 1976. Haplodiploidy and the evolution of the social insects. *Science 191*: 249–263.

Ward, S.A. and P.F. Kukuk, 1998. Context-dependent behavior and the benefits of communal nesting. *Am. Nat. 152*: 249–263.

Wcislo, W.T. and B.N. Danforth, 1997. Secondarily solitary: the evolutionary loss of social behavior. *Trends Ecol. Evol. 12*: 468–474.

Wcislo, W.T., M.J. West-Eberhard and W.G. Eberhard, 1988. Natural history and behavior of a primitively social wasp *Auplopus semialatus*, and its parasite, *Irenangelus eberhardi* (Hymenoptera: Pompilidae). *J. Insect Behav. 1*: 247–260.

Wcislo, W.T., R.L. Minckley and H.C. Spangler, 1992. Precopulatory courtship behavior in a solitary bee, *Nomia triangulifera* Vachal (Hymenoptera, Halictidae). *Apidologie 23*: 431–442.

Wenzel, J., 1991. Cooperative foraging, productivity, and the central limit theorem. *Proc. Nat. Acad. Sci. USA 88*: 36–38.

West-Eberhard, J.M., 1987. Flexible strategy and social evolution. In: *Animal Societies: Theories and Facts* (Y. Itô, J.L. Brown and J. Kikkawa, Eds.), Japan Scientific Societies, Tokyo. pp. 35–51.

Young, A.M., 1985. Notes on the nest structure and emergence of *Euglossa turbinifex* Dressler (Hymenoptera: Apidae) in Costa Rica. *J. Kansas Entomol. Soc. 58*: 538–542.

Zucchi, R., S.F. Sakagami and J.M.F. de Camargo, 1969. Biological observations on a neotropical parasocial bee, *Eulaema nigrita*, with a review of the biology of Euglossinae (Hymenoptera, Apidae). A comparative study. *J. Fac. Sci., Hokkaido Univ., Ser. VI Zool. 17*: 271–382.

To access this journal online:
http://www.birkhauser.ch