JOURNAL OF THE KANSAS ENTOMOLOGICAL SOCIETY
74(3), 2001, pp. 142–165

Nest Architecture and Nesting Ecology of the Orchid Bee *Eulaema meriana* (Hymenoptera: Apinae: Euglossini)

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ABSTRACT: The orchid bees (Euglossini), found only in the New World tropics, are among the most spectacular of the bees, with their relatively large size, brilliant metallic coloration and exceptionally long tongues thought to have evolved as an adaptation for nectar collection from long-corolla flowers. In spite of their flamboyant appearance they are exceedingly difficult to study in nature, and therefore most aspects of their biology are little understood. Here we present new data on the nest structure and nesting ecology of *Eulaema meriana* (Olivier), one of the largest and most widely distributed of the orchid bees. We describe a method for observing field nests in situ, which enabled us to examine the process of construction of six nests found in the Amazonian region of Ecuador. We study the foraging activity patterns and array of resources brought to the nest by females engaged in brood-cell construction and provisioning, and we investigate the time expenditures and time course for cell construction, larval provisioning and oviposition. We also provide a list of the natural enemies reared or collected from the nests. Our observations suggest that there may be considerable plasticity in the social organization of *E. meriana*, ranging from small single-female nests to large nests with more than one female and a possible division of labor. These observations of *E. meriana* provide a framework for comparison with other species of *Eulaema* in an evolutionary context.

Orchid bees (tribe Euglossini) are in a special position to illuminate the study of evolution of eusocial behavior in the bees. They are a mostly solitary group, although some species occasionally exhibit rudimentary levels of sociality, such as communal nesting in which two or more females of the same generation share a domicile (Zucchi et al., 1969; Santos and Garófalo, 1994; Garófalo et al., 1998; Nates-Parra and González, 2000, and references therein). Division of labor has never been reported directly in these species although guarding has been suggested in *Eulaema*, the large orchid bee (Dodson, 1966). Euglossini are part of a monophyletic group known as the corbiculate bees (manifesting a corbicula), which also include the bumble bees, stingless bees and honey bees. Therefore, the closest relatives of euglossines are the eusocial bees (Roig-Alsina and Michener, 1993; Mardulyn and Cameron, 1999; Cameron and Mardulyn, 2001). In this regard the non-eusocial euglossines are an enigma.

The orchid bees offer the only opportunity among the corbiculate apines to examine putative early stages in the development of sociality. *Eulaema* are especially useful for study in this regard. Because they are large and conspicuous, nests are relatively easy to find. They also exhibit phenotypic plasticity in nesting biology and nest sharing among females (Zucchi et al., 1969) so that comparative studies may have evolutionary significance. Yet in spite of their flamboyant appearance, there is a paucity or complete lack of biological data for many of the species. Sparse observations have led to different interpretations of even the most fundamental behavior, from mating systems (Dodson, 1975; Kimsey, 1980; Stern, 1991; Stern and Dudley, 1991) to social organization (Garófalo et al., 1998). Nest descriptions exist for a few species (Sakagami and Michener, 1965; Bennett, 1965; Dodson, 1966; Zucchi et al., 1969; Roubik, 1990; Santos and Garófalo, 1994) and even less is known of their nesting behavior and bionomics (i.e., nest architecture, foraging activity, natural enemies) or rudimentary social organization.

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Here we present new data on the nest structure and nesting ecology of *Eulaema meriana* (Olivier), one of the largest, most widely distributed and chromatically polymorphic of the large orchid bees (Dressler, 1979). We describe the architecture of nests found in the Amazonian region of Ecuador, and illustrate a method for observing them in situ. We examine the foraging activity patterns and array of resources brought to the nest by females engaged in brood-cell construction and provisioning. We investigate the time expenditures and time course for cell construction, larval provisioning and oviposition, and estimate egg to adult developmental rates. We also provide a list of the natural enemies collected from the nests. Ultimately, we infer that there is the potential for considerable plasticity in the social organization of *E. meriana*, ranging from small single-female nests to large nests with more than one female. The evidence suggests that females sharing a nest are from the same generation (thus no overlap between parent and offspring), living parasocially (Michener, 2000), perhaps with rudimentary division of labor.

Methods

We observed aspects of the nesting biology of *E. meriana* including all stages of nest development, from nest foundation and brood cell initiation to development and emergence of offspring. This allowed us to construct an activity budget for egg-laying females and assess the amount of work (time and number of trips for cell construction and food collection) required to produce a single offspring. We then determined the mean number of offspring produced per female and identified parasites responsible for brood mortality. Our study is based on the examination of females from six nests observed under natural conditions in the field.

Study site

Nesting biology of *E. meriana* was studied at the Tiputini Biodiversity Station (TBS), situated along the Tiputini River, Orellana Province (previously Napo Province), northeastern Ecuador (00°38′18″S and 76°09°00″W; elevation 215 m) between 19 June and 28 July 2000. This period corresponds to late rainy or early dry season, although this year experienced a long rainy season that extended several weeks beyond its usual time period (February through July, precipitation >3000 mm). The dry season extends from August to January (<1000 mm). There are two peak flowering episodes, one at the beginning of the rainy season and a second at the end. TBS is covered by relatively pristine lowland tropical wet forest of the Amazon Basin, and is characterized by a mean annual temperature between 25°C and 27°C.

Nests examined

From 19 June to 28 July, over a period of 40 days (240 hours of observation), we observed six nests in their natural locations inside harvested *Iriartea* palms or within the walls of wooden buildings at TBS. Three nests (*Meyer*, *Enrique* and *Lab*) were observed from initiation to completion of one to four cells, and three others (*Comedor*, *Susanna* and *Lizard*) were studied in the middle or late stages of construction and provisioning. Table 1 indicates the identity of each nest, its specific location, total number of cells in the nest and dates of study. All but the *Enrique* nest were eventually collected and brought to the laboratory for measurement or dissection after the resident females failed to return to the nest. The *Lab* nest female was collected and deposited in 95% ethanol as a species voucher. We measured cell height and diameter (top and middle of cell), thickness of the cell cap, walls and floor, and counted the total number of sealed and open cells. We also measured

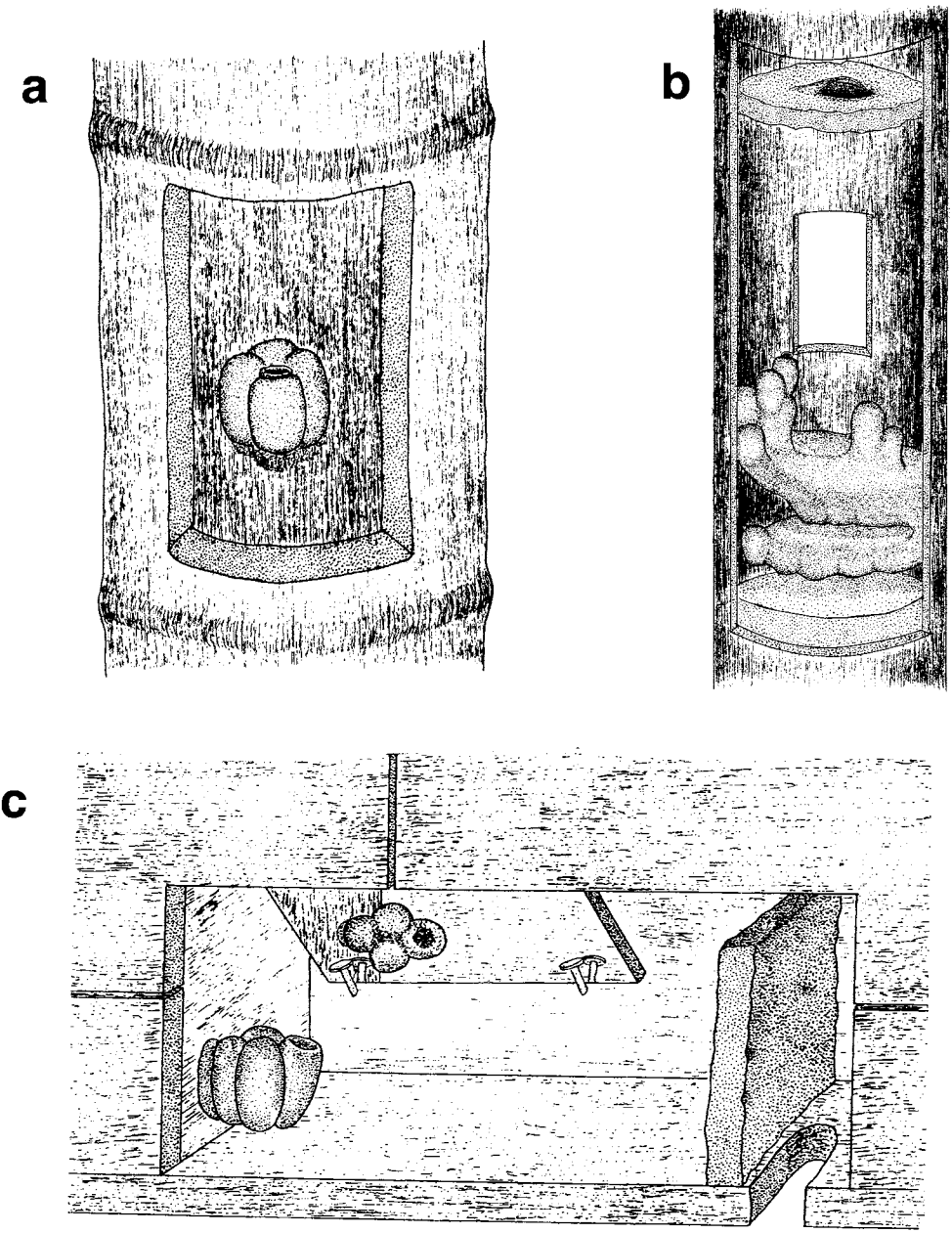

Fig. 1. Drawings of *Susanna* (a), *Comedor* (b), and *Enrique* (c) nests *in situ*, showing observation windows. Internal diameter of *Susanna* nest cavity = 13.5 cm, diameter of *Comedor* cavity = 17.5 cm; length of *Enrique* nest cavity = 40 cm

depth, weight and volume of cell provisions. Two nests (*Comedor* and *Lizard*) were left undissected at ambient temperature to obtain estimates of offspring development times and to identify any brood parasites. Size of each nest cavity (total cavity area in which nest was found) was measured to the nearest cm.

Observations of cell construction and foraging

To observe nest-building behavior in situ, we cut observation windows into three nests (Fig. 1). This involved the use of a hand-saw and machete to carefully cut through a wall of the nesting chamber (a palm tree or wall of a wooden building) while the female was away from the nest. Plexiglas (2 mm thick) was cut to fit snugly into the opening and the piece of wood cut from the chamber wall was used as a cover to keep the nest dark when not under observation. Window dimensions for the three nests: *Comedor*, 9 cm × 16 cm; *Susanna*, 9 cm × 18 cm; *Enrique*, 24 cm × 8 cm. A video camera (Canon GL1 Digital Camcorder) with hand-held halogen flashlight was used to record nest-building behavior directly through the window. In one of the five observation nests (*Enrique* nest) the brood cells were hidden in shadow below the window. To observe the cells without disturbing the female, a mirror (9 cm × 7 cm) was set in place above the cells at a 45° angle, which reflected the nest so that it could be seen clearly through the Plexiglas window (Fig. 1c). The camera was hand-held or placed on a tripod (Manfrotto with fluid head # 3063). Observations on the *Enrique* nest were made continuously from sunrise to sunset to record each entry and exit from the nest, beginning with nest initiation and continuing through cell construction (4 cells) and oviposition (3 cells). Additional observations were made inside the nest at night, covering an entire 24-hr period, to record cell construction and oviposition. Exit and entry times were taken with a hand held stopwatch. Foraging trips and nesting behavior at the other nests were recorded daily during one-to several-hour stretches. Females entering and exiting from a nest were extremely sensitive to disturbance, so care was required when recording foraging behavior; we stood at least 3 m away from a nest entrance during these times. Observations terminated when a foraging female failed to return to her nest. Material carried back to the nest in the corbiculae was distinguished by color, consistency and load size: pale yellow indicated pollen, large clumps of red, brown or gray material indicated mud, smaller clumps of wet black or dark gray material indicated feces, and smallish dark gray material indicated resin. The identity of each load was verified by following a female's activity in the nest after depositing the load and, in some cases, by removing a sample of the load from the nest after her next departure.

Flowers visited by *E. meriana* near nest sites were collected and later identified to genus by Helen Kennedy (University of British Colombia). Voucher specimens of bees, nests and flowers are deposited at the Illinois Natural History Survey, University of Illinois at Urbana–Champaign.

Statistical analyses

Differences in the length of foraging trips for different resources (pollen, mud, feces and resin) were assessed with a single-factor analysis of variance (ANOVA) and a Tukey multiple comparison test. Differences in the number of foraging trips for each resource were also tested with a Chi-square Goodness-of-Fit test. Testing equality of variances of cell volumes was done by Levene's test using JMP (Version 4.04, SAS Institute Inc., Cary, NC). All other analyses were implemented in SPSS version 7.5.

Results

Nest sites

Four nests were initiated and two were under protracted construction toward the end of the rainy season inside pre-existing cavities in hollow *Iriartea* palms or within the empty space between the outer and inner walls of double-walled buildings (Table 1, Fig. 1). No

Table 1. *Eulaema meriana* nests observed at the Tiputini Biodiversity Station in Ecuador.

Nest	Location	Total # cells	Observation dates
Meyer	Inside drawer beneath staff dormitory floor beams	2	6/19–7/8 2000
Comedor	*Iriartea* palm cut for dining room support beam	76	6/24–7/14 2000
Susanna	*Iriartea* palm cut for researcher dormitory support beam	4	7/8–7/12 2000
Lizard	*Iriartea* palm cut for laundry room support beam	14	7/8 2000
Lab	Under roof molding of laboratory building	1	7/10–7/19 2000
Enrique	Within outer wall of student dorm, 10 m from *Enrique* 1	4	7/14–7/28 2000

subterranean nests were found, and no burrowing or cutting of material within the nest cavity took place. Figure 1 illustrates the general habitus, including the location, cavity dimensions and entrance of three study nests (*Comedor*, *Susanna* and *Enrique* nests). Most nests were built between 60 and 90 cm from the ground surface; the *Meyer* nest was started in an abandoned drawer stored beneath the floor boards approximately 1.5 m from the ground surface, and the *Lab* nest was built under a roof molding about 4.5 m above ground. See Appendix 1 for additional data on cavity positions and dimensions.

Nest architecture

All nest entrances, except the *Susanna* nest, were modified by construction of a mud wall or ceiling (8–9 mm thick, $n = 3$) at the point of entry (Fig. 1), with a narrow entrance hole (15 mm diam.) through the mud wall. The size of the wall or ceiling was considerable in some nests. The *Comedor* ceiling measured 17.5 cm in diameter and had an additional portico above the main ceiling (2 cm high × 7 cm wide). A mud wall (4.8 cm high × 0.7–1.4 cm thick × 40.7 cm total length) surrounded three sides of the *Meyer* nest. This wall structure took between 3–4 days to complete by a solitary foundress.

E. meriana nests consist of a pedicel, constructed of mud attached to the wall or floor of the nest cavity, and a variable number of partially fused urn-shaped brood cells (Fig. 2). The size of the pedicel can be considerable, and increases with the overall size of the nest (single-cell stage: 2.8–3 cm length, 1.8–2 cm width, 0.4–0.5 cm thickness; 76–cell nest: 8.5 × 5 × 1.3 cm). The pedicel is constructed first and its anterior surface forms the back wall of the first brood cell. The cell is large (mean length 29 ± 1.4 µl, Table 2, Appendix 1; mean volume 4.8 ± 0.14 ml, Table 3) and composed of a thick layer of mud (Table 2) that hardens to a dense clay-like consistency when dry, like an earthenware pot. Cells are remarkably similar, even from nest to nest (Table 3, Appendix 1). Within the 3 levels of the *Comedor* nest (Table 3), variances of cell volumes were not significantly different ($P = 0.468$, Levene's test); neither were they significantly different among the *Enrique*, *Lizard*, and *Susanna* nests ($P = 0.954$, Levene's test). Each successive cell is fused to the long surface or wall of the previous cell, which becomes part of a wall of the new cell (Fig. 2b). New cells are frequently attached along the same plane, with the point of attachment at or near the base of the previous cell (Fig. 2c, d), although this is not always the case (Fig. 2e, top layer). Cells are usually overlaid with a thin, patchy application of feces and lined with resin, which extends beyond the mouth of the cell to form a pliable collar (1 mm thick × 3.5 mm high, Table 2) (see open cells, Fig. 2b–e). Immediately after oviposition the collar is pushed inward to form a cap, which is overlaid with a layer of, mud (7–8 mm thick, Appendix 1). In larger nests, such as the *Comedor* nest, once a layer of cells is complete (expanded to fill the cavity space in the horizontal dimension), the apical surface of those cells is covered with a layer of mud, giving the appearance of a thick

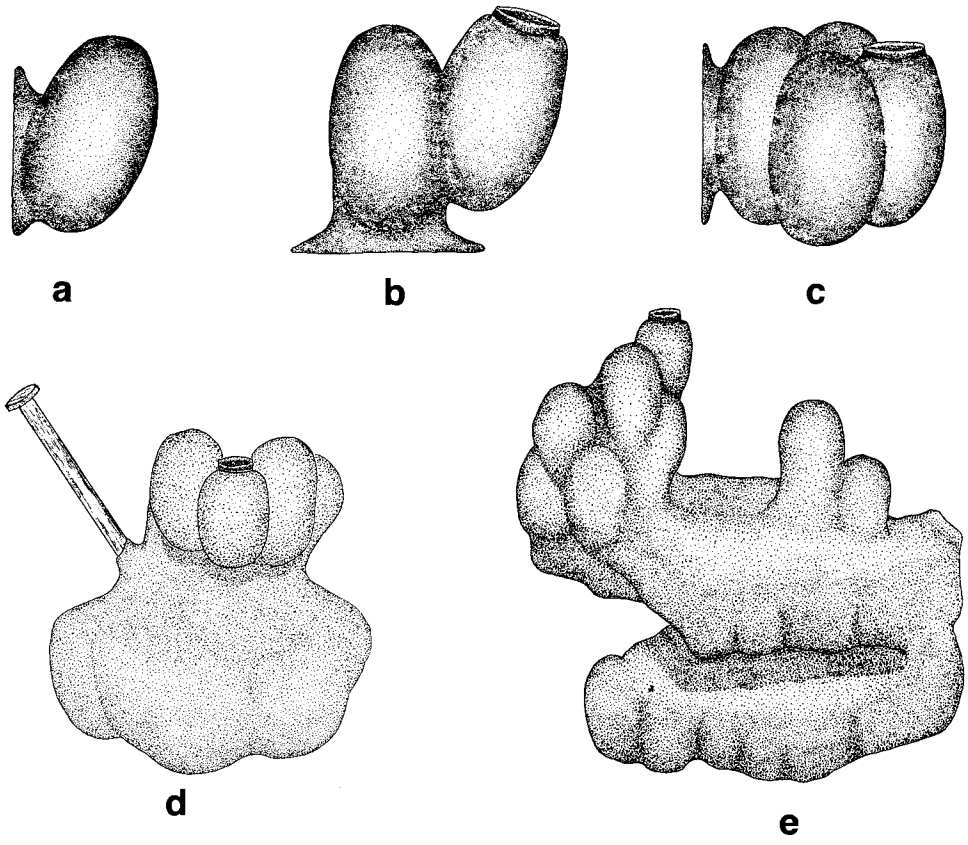

Fig. 2. Brood cell configuration of the six *E. meriana* nests used in this study: *Lab* (a), *Meyer* (b), *Susanna* and *Enrique* (c), *Lizard* (d) and *Comedor* (e). See Appendix 1 and Fig. 1 for nest and brood cell dimensions.

floor upon which the next layer of cells is built (Fig. 2e). A thick vertical wall or pillar of mud separated the bottom and middle levels of the *Comedor* nest at the pedicel end (Figs. 1b, 2e). The pillar and pedicel supported the middle cell layer, and a third (top) layer of cells was begun directly atop the middle layer.

Cell 1 of the *Meyer* nest (Fig. 2b) was built upon a mud pedestal constructed on the wood substrate of an abandoned drawer, located in the crawl space beneath the floor of a dormitory. A second cell was attached near the base of the first and extended at a slight

Table 2. Dimension and thickness of brood cell components.

	Average (mm) $n = 30$
Cell length	29 ± 1.4
Cell diameter top	12 ± 1.1
Cell diameter middle	16 ± 0.68
Mud thickness top	7 ± 1.4
Mud thickness side	2.8 ± 0.9
Mud thickness bottom	6 ± 3.3
Resin collar thickness	* 1 ± 0.0
Resin collar height × diameter	* 3.5 ± 0.7 × 11.5 ± 0.7

* Indicates a sample size of only 2 cells.

Table 3. Comparison of brood cell volumes (means and standard deviations) for the three different layers of cells in the *Comedor* nest and for the *Enrique*, *Lizard* and *Susanna* nests. Within the 3 *Comedor* layers, the variances were not significantly different ($P = 0.468$, Levene's test), neither were they significantly different among the *Enrique*, *Lizard* and *Susanna* nests ($P = 0.954$). For the variances of the 6 nest-layer combinations, $P = 0.013$.

Nest	Layer	*n*	Mean (µl)	SD (µl)
Comedor	Bottom	17	4810	158
Comedor	Middle	14	4628	123
Comedor	Top	3	4770	227
		n	Mean	SD
Enrique	1	4	4990	42
Lizard	1	4	4700	56
Susanna	1	4	4937	48

angle from its shared wall. The first cell was closed after oviposition, but the second remained open, as the female had not yet oviposited before abandoning the nest. Appendix 1 provides comparative data on the total number of cells and mean cell dimensions for each nest.

Larval provisions and cell construction materials

Each brood cell was mass provisioned to approximately two-thirds of its volume with a pale, creamy-yellow, extremely sticky pollen/nectar substance, giving the appearance of creamed honey. Appendix 2 gives comparative quantities (depth, weight, volume) of cell provisions for four nests relative to the size (internal height and diameter) of each cell. Females returning to their nest with this sticky pollen mass attached to their corbiculae deposited it directly into a brood cell, often checking first inside the cell before backing into it to unload the pollen from their hindlegs. A ritualized movement follows pollen removal, in which a female makes a rotation, from 1 to 1.5 turns, with her abdomen, mid- and hindlegs fully inside the cell and her forelegs grasping the lip of the resin collar. With these motions, the female appears to be tamping down the cell contents.

Other collected materials are deposited in the nest, including mud, feces and resin. Mud and feces are deposited directly onto the floor of the nest in a single pile near the nest pedicel. Resin is deposited separately and is usually stuck onto the cavity wall near the pedicel. Mud was often collected nearby, within 5–20 m of the nest, allowing observation of the mud-collecting behavior. Females collect a lump of mud with their mandibles while on the ground. Then while hovering a few cm above the surface, the mud is transferred to the foreleg, then midleg and ultimately to the hindleg, where it is packed onto the corbicula. Each newly gathered lump of mud is packed alternately onto one corbicula then the other, until both legs are fully loaded. Each corbicula is packed with 5–6 roughly spherical lumps (6–7 mm diam., 0.035–0.04 g) before a female returns to deposit the mud into the nest. Foraging in the field for feces and resin were never directly observed. The load dimensions were generally smaller than for those of mud, but the load weights (dry weights) were about the same for feces and mud.

Foraging activity

Foraging activity of females was studied primarily at the *Comedor* and *Enrique* nests, with additional data collected from *Meyer*, *Susanna* and *Lab* nests. Females foraged for pollen and nectar, mud, feces and resins. Pollen and nectar are mixed together and brought

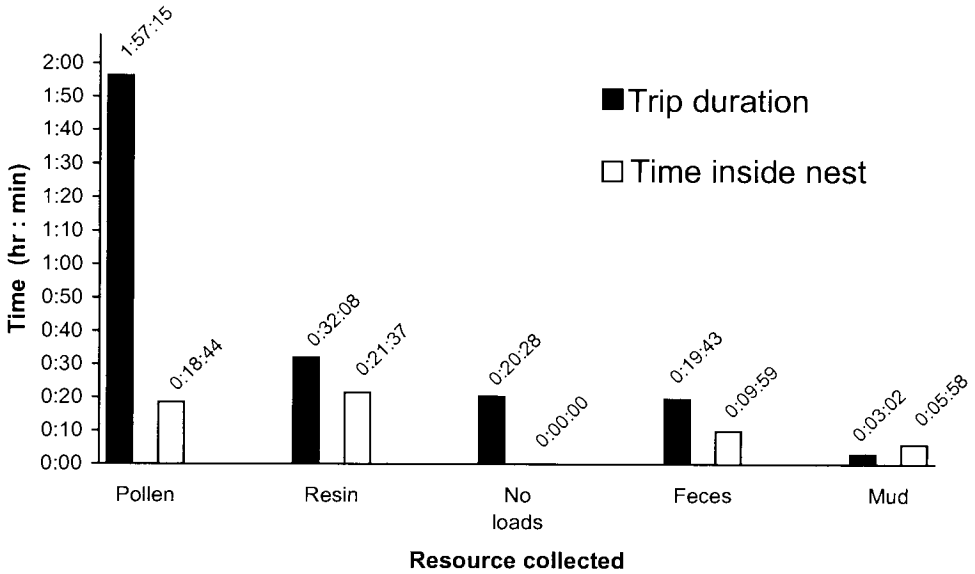

Fig. 3. Mean trip duration for each resource and mean time spent inside the nest after returning with each resource; data averaged over all six observation nests.

back to the nest on the corbiculae, as are the other materials. Trip lengths varied significantly ($P < .0001$, ANOVA), depending on the material collected. Pollen/nectar-collecting trips last on average about 2 hours (1:57:15 ± 0:29:09, $n = 33$) and are significantly longer than trips for other resources ($P < 0.0001$, Tukey test) (Fig. 3). In contrast, mud-collecting trips take only a few minutes (0:03:02 ± 2:37, $n = 239$) and are significantly shorter than trips for pollen/nectar ($P < 0.001$) and resin ($P < 0.03$) but are statistically equivalent to trips for feces ($P > 0.5$). Resin and feces trips average 0:32:08 ± 0:23:56, $n = 19$ and 0:19:43 ± 0:14:10, $n = 13$, respectively (Fig 3). A small fraction of the time (0%–8%) a female returns without any material in her corbiculae. These trips last about 20 min (±12 min, $n = 14$).

There is a specific chronology to the collection of these different materials, depending on the time of day (Fig. 4, Appendix 3) and particular stage of cell construction (Fig. 5a–c). Pollen/nectar is collected from dawn to about noon and mud is mostly collected in the afternoon, as are feces and resin (Fig. 4). Nest initiation begins with mud collection for the construction of a mud wall and entrance, pedicel and first brood cell. The wall and entrance modification may take as little as one day (*Enrique* nest) or up to four days (*Meyer* nest) to complete. All trips on day 1 of cell construction are devoted exclusively to mud collection (Fig. 5a). By the second day of cell construction, the cell is nearly complete and the female spends approximately equal time collecting mud and resin, of which the latter is used for the cell lining. On day 3 almost no mud is collected; instead about 70% of the foraging effort is devoted to larval food collection and about 20% to resin collection. Activity on day 4 follows a similar pattern to that of day 3 (Fig. 5a), and oviposition occurs during the evening of the fourth day. On some trips the female returns without any material in the corbiculae. These are usually in the late afternoon and often on the last trip of the day (Fig. 4). The construction and provisioning of successive cells (Fig. 5b, c) follows a similar pattern, although the percentage of time devoted to mud collection is reduced and

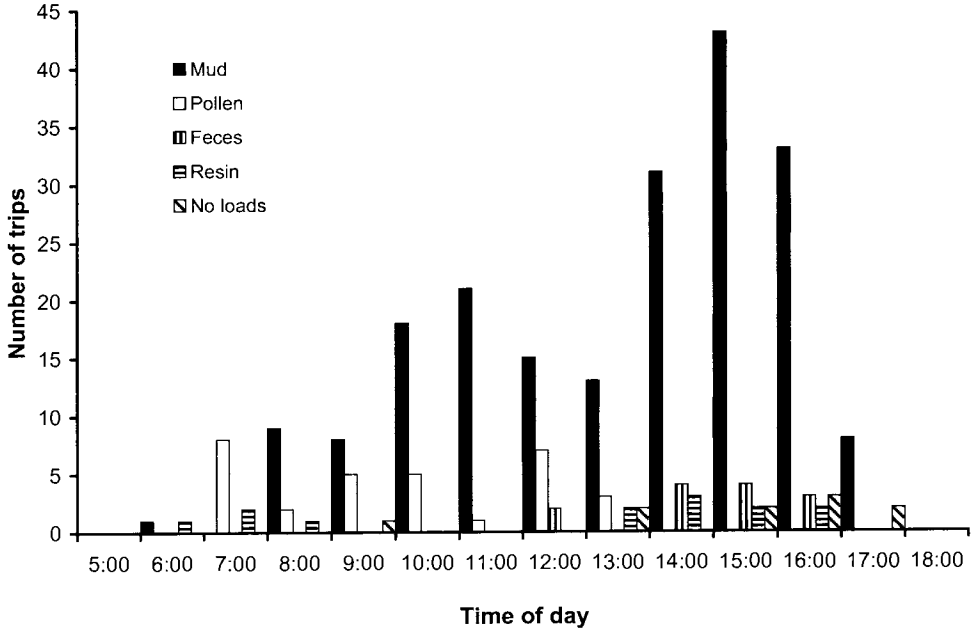

Fig. 4. Mean daily foraging activity of *E. meriana*, averaged over all observation days of the *Enrique* and *Comedor* nest females. See Appendix 3 for total time estimates each bar depicts.

more effort is given over to pollen/nectar collection sooner in the cycle. Mud only is collected on the first day for cells 2 and 4, as for cell 1, but day 2 is already devoted almost exclusively to pollen/nectar collection.

After the first oviposition, it appears that less time is required to build and provision the successive cells. Time to oviposition for cell 1 of the *Enrique* nest was 5 days; cell 2 was 4 days, cell 3 was 2–3 days. The female disappeared before ovipositing into cell 4, but based on the quantity of provision in the cell, it appeared that she would have oviposited at the end of the second or third day. Cell 4, which appeared to be fully provisioned at the time of abandonment, was built and provisioned over a 43-hr period (Fig. 5c).

Relative effort in terms of total number of trips devoted to the collection of each resource (Table 4) varied significantly for a given brood cell ($P < 0.0001$, Chi-square), and with each successive cell (all resources $P < 0.001$, except feces, $P = 0.0498$, Chi-square). For instance, the *Enrique*-nest female made 103 mud-collecting trips to build the pedicel and first cell but only half that number was required for the second brood cell (Table 4). The number of trips devoted to collecting materials for cell construction, principally mud, versus larval food was 10:1 (Table 4). In contrast, the proportion of time spent collecting mud versus larval food was equal or greater for food (Fig. 5, Appendix 3). Total time devoted to collecting construction materials was about 11:35:00 hours for the first brood cell, 6:22:00 hours for cell 2 and 5:58:00 hours for cell 4. Total time to provision a cell with pollen and nectar was 19:33:00 hours for cell 1 and 21:08:00 hours for cell 2 (cell 4 abandoned before oviposition).

The amount of time spent in the nest between trips varied with the resource collected ($P < 0.0001$, ANOVA) (Fig. 3). Twice as much time was spent in the nest after pollen and resin trips (about 20 min) than after mud (about 5 min) and feces trips (about 10 min). These differences were significant only between time in the nest after pollen/nectar collection versus mud collection ($P < 0.0001$, Tukey test).

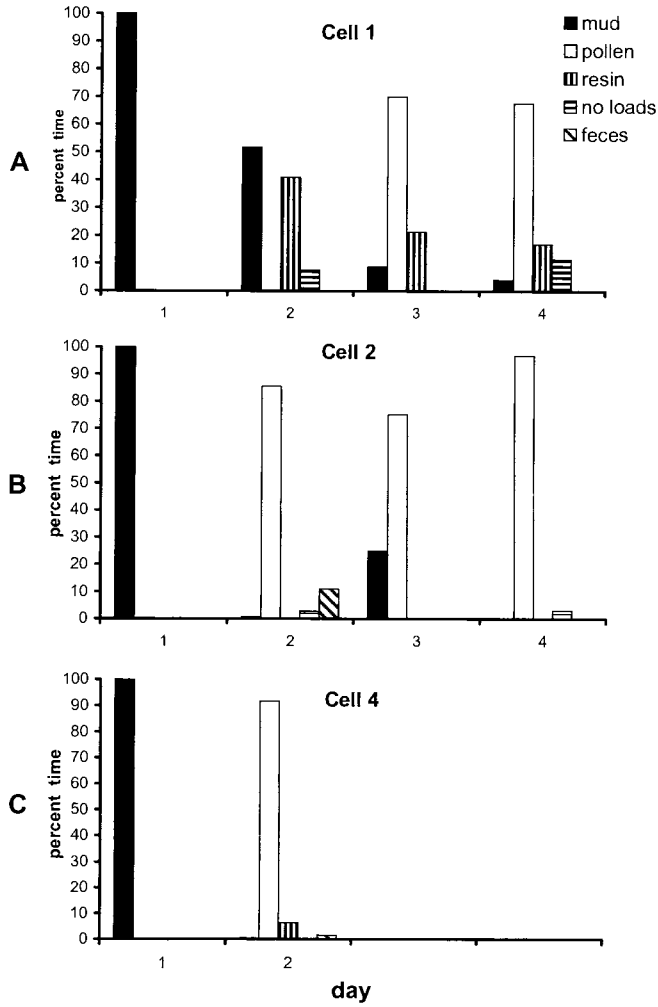

Fig. 5. Percent time collecting each resource for cells 1 (a), 2 (b) and 4 (c) of the *Enrique* nest.

Number of cells per female

Females constructed and provisioned an average of 4 cells before disappearing from the nest. The *Enrique*-nest female spent 18 days on her nest, from its initiation to the provisioning of a fourth cell, before disappearing. The *Susanna*-nest female was found dead in

Table 4. Number of collecting trips for each resource (mud, pollen, resin, feces, no loads = nectar), for each successive brood cell in the *Enrique* nest.

	Mud	Pollen	Resin	Feces	No loads
Cell 1	103	8	7	0	4
Cell 2	56	12	2	3	2
*Cell 4	42	3	2	5	0
Total	201	23	11	8	6

Note: *The female disappeared before oviposition into cell # 4, although it appeared to be nearly fully provisioned at the time of departure, based on the depth of pollen provision (see Appendix 2). Only sporadic observations were made during construction and provisioning of cell 3 and these are not shown here.

her nest during the provisioning of a fourth cell and, likewise, the female from the *Comedor* nest disappeared just before ovipositing into the last open cell of a cluster of five cells. The *Lizard* nest contained an uppermost layer of seven cells. The *Lab* and *Meyer* nests contained only one or two cells because the females were disturbed before nest building completed its normal course.

Nocturnal activity— oviposition and cell construction

All females work inside the nest during the night with few or no resting periods. Cell construction often occurs at night after the stockpiling of mud collected during the latter half of the day. Oviposition occurred at night in every nest in which oviposition was observed directly (*Comedor* and *Enrique* nests) or known to have occurred (*Lab* nest). One large egg (7 mm long in *Lab* nest) is laid in each provisioned cell. Based on observations of the *Enrique* nest, oviposition occurs after several hours of preparatory work inside the cell. This work included the apparent tamping of provisions with the abdomen or head inside the cell, and long hours devoted to work on the cell itself with the head inside. The latter could have included final completion of the cell lining. Oviposition (*Enrique* and *Lab* nests) or attempted oviposition (*Comedor* nest) occurred between 1600 and 2300 (n = 5). The actual egg-laying event took less than a minute, as the female backed into the cell grasping the collar with her forelegs. Immediately after withdrawing her abdomen she placed her head inside the cell momentarily, withdrew it and began to close over the cell with the resin collar, using her forelegs and mandibles. After several minutes on this task she spent two to three hours covering the top of the cell with mud (7–8 mm) and smoothing this over after each application. Several hours were thus devoted to oviposition and cell closure, after which the female began to work on the construction of a new brood cell. In the case of cell 3 of the *Enrique* nest, a fully formed (although unlined) cell was constructed and at least partially lined between 1730 and 0630 (13 hours) the following morning.

Division of labor

Five of the six study nests contained a single female, and three of these (*Meyer*, *Lab* and *Enrique*) were observed during the nest initiation process. The *Lizard* nest, containing two layers of brood cells may have been established by a different female than the one we observed at the time of our study. Only the large *Comedor* nest had more than one female during our study. Two females were together in the *Comedor* nest for a period of at least 17 days (24 June–10 July) after the nest was first discovered. The following are observations made inside this nest (10 July) the day after the Plexiglas window was inserted. One of the females entered the nest with pollen-nectar loads on her corbiculae and an orchid pollinium attached to her vertex. She deposited the provision into the only open cell, this being one of a cluster (or tower) of five cells built atop the middle layer (Fig. 2e). Three other cell towers had been constructed before observations began; two were adjacent and consisted of three cells each, the third had four cells (Fig. 6-top). A second female inside the nest carried mud in her mandibles and was sealing up cracks along the margins of the Plexiglas window. She was also observed carrying mud from the stockpile to the central floor of the nest cavity where several dead females lay. She was in the process of covering one of these with a layer of mud, making repeated trips from the stockpile of freshly collected mud to the dead female. Thus two females shared a nest that contained only a single uncapped brood cell; one female collected larval provisions while the other worked inside the nest with mud. The following day, only the pollen-collecting female (with the attached pollinium) remained. Over the following four days, before she disap-

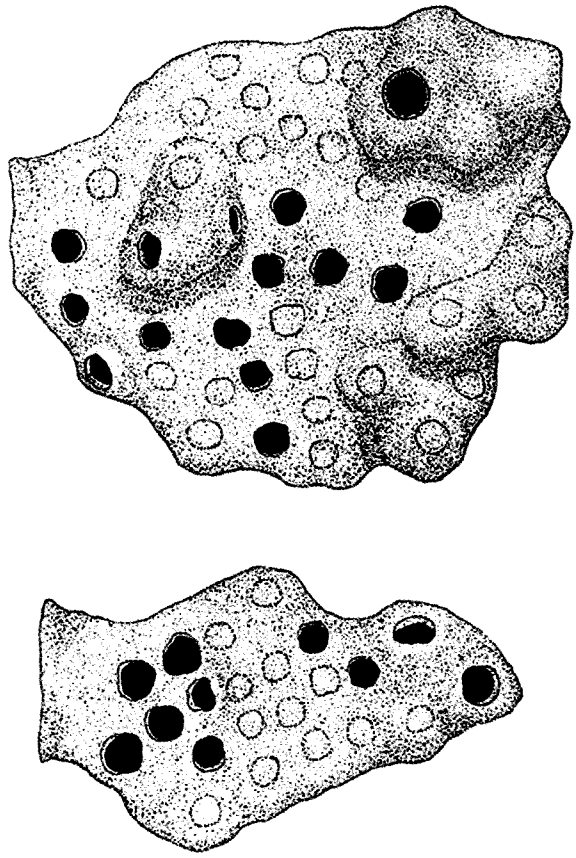

Fig. 6. *Comedor* nest drawing showing emergence holes (black circles) and capped, empty cells (open circles). The drawing divides the nest into two parts: (bottom) depicts bottom layer; (top) depicts middle layer and cell towers of the top layer.

peared from the nest in a rainstorm, this female continued to collect pollen, feces and resin and to work on the cell. The evening before disappearing she appeared to be ready for oviposition inside the open cell. An exposed egg protruded slightly from the tip of her abdomen as she expanded and contracted the metasoma while rotating around the cell opening.

Cavity and nest reuse

The *Enrique* nest was initiated in an abandoned nest cavity previously used by another female, presumably of the same species judging by the similar architecture of the abandoned brood cells that lay on the cavity floor. This was an old cluster of five cells, four of which were empty with their caps off at the time of the new nest founding. The cells were not decomposed and there was no fungal decay. The *Comedor* nest was obviously expanded over several non-overlapping generations. On the floor of this nest lay three dead females in different states of decomposition, two were interred within a layer of mud (see above). Many empty cells were capped with a layer of mud, presumably sometime after adult emergence (Fig. 6). 12 of the 21 cells of the bottom layer were capped and empty

(Fig. 6-bottom); and approximately 25 of the 40 cells of the middle layer were similarly capped (Fig. 6-top). It appears that brood cells are not reused.

Offspring development

Adults emerge from the cell through the cap (operculum) covering the top of the cell. Time from oviposition to adult emergence from cell 1 of the *Enrique* nest was 137 days *in situ* in the field. The actual emergence was not witnessed hence the gender is unknown. Inferred development time for an adult male emerging from the final cluster of cells of the *Comedor* nest was 101 days. The first 34 days were in situ; the remaining 67 days were in the laboratory in Amazonian Peru (20 days) and in the USA (47 days in a greenhouse). Approximately seven weeks after removing the nest from the field (21 September 2000), 10 *E. meriana* adults (9 males, 1 female) emerged over a 2-week period. Prior to the bee emergences, six meloid beetles emerged (discussed below). We determined the contents for most of the 76 cells, according to each layer (Fig. 6): bottom layer [total 21 cells, 12 capped and empty, 6 meloid emergences, 4 open and unaccounted for]; middle layer [total 40 cells, 25 capped and empty, 9 *E. meriana* emergences, 6 open and unaccounted for]; top layer (the 4 towers) [total 15 cells, 1 *E. meriana* emergence, 1 open pre-oviposition, 13 closed with contents undetermined].

From the *Lizard* nest, two females emerged from the top layer of 7 cells (8 Nov and 13 Nov, respectively) 13–14 weeks after removal from the field; one dead male was removed from a cell of the bottom layer. Two other cells of the bottom layer produced separate emergences of leucospid wasps (discussed below).

Nest parasites, scavengers and associates

COLEOPTERA: *Meloetyphlus fuscatus* Waterhouse (Coleoptera: Meloidae) emerged from the *Comedor* nest. A total of 3 males and 3 females emerged from the middle layer of brood cells between 25 August and 1 September 2000.

HYMENOPTERA: Two individuals of *Hoplomutilla conspecta* Mickel (Hymenoptera: Mutillidae) were seen inside different nests during field observations between 10–11 July 2000. One was observed on the lower tier of the *Comedor* nest, chewing at the underside of a closed brood cell of the middle layer. She left the nest without making a hole in the cell and was not seen ovipositing in the cell. A second individual was seen inside the *Susanna* nest.

Wasps of the family Leucospidae (*Leucospis, cayennensis* species group) emerged from two distinct emergence holes (2 mm diameter) in two lower cells of the *Lizard* nest. The first emergence occurred 46 days after removing the nest from its field location, and produced 22 females and 6 males. A week later (19 September 2000), a second emergence produced 18 females and 5 males from a single emergence hole in a second cell. Thus a total of 51 wasps emerged from this nest, which contained only 13 closed cells, three of which yielded adult bees. Dissection of one of the cells revealed the presence of at least 20 *Leucospis* pupal exuviae. There is no doubt that this parasitoid is gregarious.

SCAVENGERS AND OTHER ASSOCIATES: Two or three cockroaches were seen inside the *Comedor* nest between 11–13 July 2000. They appeared to be interested only in the pollen/nectar provisions within the open cell. On several occasions when the female was away from the nest one was seen with its head inside the cell.

The *Lizard* nest was discovered (8 July) after a Forest Whiptail lizard (*Kentropyx pelviceps* Cope, family Teiidae) was found trapped just inside the nest entrance at the top of an *Iriartea* palm, half of its body protruding from the top of the palm. This large lizard had

presumably entered from the top of the palm and became stuck in the narrow opening of the mud ceiling on its way out. The returning resident female discovered the lizard and attempted to "pull" it out, to no avail. When after several hours her attempts failed, she abandoned her nest. The lizard was forcibly removed by an assistant and escaped. The resident *Eulaema* female was seen entering and leaving the nest early the following morning but failed to return afterwards, and was not seen again. Three days later, three newly laid lizard eggs were found on the floor of the palm cavity of the *Susanna* nest. These were approximately an inch long and half an inch in diameter, pale gray with small speckles. These eggs may have been laid by *Kentropyx pelviceps*.

Discussion

Nest site preferences

All *E. meriana* nests observed in our study were constructed in artificial preexisting cavities above ground, including harvested *Iriartea* palms and the wall spaces of buildings. Unpublished reports (C. Skov, unpubl. data; C. Dodson, pers. comm.) indicate that *E. meriana* also nests in subterranean cavities but our study suggests that this may not be common. The only other published studies of *E. meriana* nests report them in above-ground cavities, one inside an abandoned ant nest attached to a tree limb (Bennett, 1965) and the other inside a hollow limb (Dodson, 1966). We do not know what cues these bees use to locate suitable nesting sites, but their selection is not particularly specialized in terms of overall cavity size and height above ground. Characteristics of the natal nest may influence the search image of new adults, for it seems unlikely that all the *Eulaema*-occupied *Iriartea* palms at TBS would have been found independently by chance alone. Learning surely influenced the *Enrique* nest female, who initially started a nest in the wall of a dormitory and then rebuilt a second nest (after being disturbed) in an identical cavity space 10 m further along the same wall. Odor cues may also have influenced site selection in this case, because the cavity contained a cluster of old brood cells from a prior occupant of the same species.

Comparative data on nest site preferences in *Eulaema* are too few to decipher species-specific patterns. However, it seems clear from published reports that, unlike *E. meriana*, *E. nigrita* prefers to nest in cavities in or on the ground (Zucchi et al., 1969; Santos and Garófalo, 1994; see review by Garófalo, 1994). This may also be true for *E. polychroma* (Nates-Parra and González, 2000). Natural nest cavities may be limiting in the case of *E. meriana*, and therefore a wide array of cavities may be satisfactory. Daily walks through different parts of the forest at TBS led to no *E. meriana* nest sightings, even though males were commonly observed at display sites on trees in different areas. Yet the density of nests around the TBS station was striking. This was obviously due to the availability of suitable man-made nesting cavities, which could have a significant effect on local population size. The six nests from our study alone would likely have produced on the order of 60–70 new adults, an estimate that assumes a 30%–40% parasitization rate. Thus artificial domiciles placed in appropriate habitat might actually attract females in significant numbers, ensuring sufficient nests for future studies. Garófalo et al. (1993) had considerable success in attracting species of *Euglossa* and *Eufriesea* to artificial trap nests placed in the field in Brasil. This could be important for future conservation efforts.

Nest architecture—variation and uniformity

It is clear that *E. meriana* modifies its nest entrances. This appears to be a facultative trait, perhaps more commonly exhibited in response to the features of man-made cavities.

All cell clumps are attached by a pedicel to the cavity wall or floor. The overall shape of the nest is probably determined by the constraints of the cavity; the *Comedor* nest was built in circular tiers, the diameter of which conformed to the internal diameter of the palm (Fig. 1b).

E. meriana nest cavities may vary in size and shape, but the brood cells of each nest are uniform in size, shape and structural components. They are made of mud and a relatively small amount of fecal material, which is dabbed here and there after the major structure of the cell is complete. All cells are lined with resin, which protrudes in the form of a pliable collar several mm above the top of the cell. After oviposition, the collar is pushed inwards and forms the basis of a cell cap upon which several mm of mud are applied. In these respects, *E. meriana* cells resemble those of other *Eulaema* species. In small nests, cells are arranged in groups of four or five, usually along a single plane. This pattern seems to conform to the comb-type of cell arrangement described by Friese (1941) and later by Zucchi et al. (1969). The larger nests are constructed in multiple layers. A layer may contain >20 cells arranged uniformly along one plane. As the nest grows, cells may become more irregularly arranged, as seen with the top layer of the Comedor nest (Fig. 2e). However, the more oblique cells on top might later get packed all around with mud, more closely resembling the even arrangement of the middle and bottom layers (Fig. 6).

The uniformity in size of brood cells may account for the fact that body size variation in *E. meriana* appears to be negligible, at least locally. This might, as Roulston and Cane (2000) suggest, be the result of strong selection on parental provisioning behavior, which primarily determines body size in bees (Johnson, 1988; Ribeiro, 1994). *E. meriana* body size is among the largest of any bee. It has been suggested that females of large orchid bees are among the most important pollinators of certain New World tropical plants (Janzen, 1971), and that the large body size enables them to travel long distances to patchily distributed flowers, each of which is small and offers relatively little food, requiring many visits from each bee to gather a full load. Males also fly long distances (Kroodsma, 1975; Janzen, 1981) and are not noticeably different in size from the females (Dressler, pers. comm.). In addition to long-distance flight, large body size allows these bees to fly in cool rainy conditions, when smaller bees are unable to do so (Cameron, pers. obs.). These fitness factors may comprise the selective regime constraining variation in body size. The mechanism may be found in cell construction and provisioning behavior, namely that females make and provision brood cells of a constant size. Brood cells within and between nests were remarkably similar in size. There were no significant differences in cell volume among the *Lizard*, *Enrique* and *Susanna* nests or within each layer of the large *Comedor* nest. However, there were significant differences among the three layers of the *Comedor* nest. Exactly how a female knows what size cell to build is not known. However, it is very possible that she uses her own body size as a guide to building the appropriate sized cell. During construction, a *E. meriana* female has her entire body inside the cell much of the time, rotating on vertical and horizontal axes, suggestive of molding the cell to her own form. A positive correlation between cell size and parent size exists in other large bees (e.g., *Centris*, Alcock, 1979).

Larval food and provisioning behavior

The food stored in the brood cells is in the form of a creamy, sticky mixture of pollen and nectar that is soft enough to conform to the shape of the cell. It comes into the nest in that form on the corbiculae of the provisioning female, so manipulation of the pollen occurs in the field, perhaps only by addition of nectar. Often, nectar alone appears to be re-

gurgitated after the last foraging trip of the day. A fully provisioned cell is approximately two-thirds full. It would be interesting to know if any glandular secretions are added to the pollen, either during manipulation in the field or after depositing it into the brood cells. The extraordinarily long time in which the female has her abdomen inside the cell, turning round and round, tamping and preparing the cell is suggestive that a glandular secretion, perhaps from the Dufour's gland, may be added to the food or the cell lining. Batra and Norden (1996) describe the use of both salivary and Dufour's gland secretions in *Anthophora*, which in combination contribute to the preservation of larval food. Salivary gland secretions apparently are commonly added to the food of the corbiculate Apidae (Michener, 2000), to which the euglossines belong.

Other materials, including mud, feces and resin, are stockpiled temporarily inside the nest for use in brood cell construction. These are not stored in separate receptacles, but are piled in a clump on the floor of the nest cavity or, in the case of resin, stuck to the cavity wall near the clump of mud.

There are too few data in our study to draw any conclusions about correlations between cell size and pollen mass. However, if the equal sized cells are filled with approximately equal amounts of pollen and nectar, as they appear to be, cell size could be the mechanism by which a female measures the amount of provision she must collect before ovipositing. This could explain why during less favorable times of the season nests (but not cells) are smaller (fewer number of brood cells) than during peak flowering periods (Santos and Garófalo, 1994). Rather than make smaller cells or provision cells with less food during unfavorable periods, females continue to provision standard sized cells with standard amounts of food, but fewer of them. In this way, mean body size can be maintained over time. A similar trend in offspring size uniformity occurs within two other corbiculate apine tribes, the highly eusocial honey bees (Apini) (Roulston and Cane, 2000) and stingless bees (Meliponini) (Waddington et al., 1986). In fact, this trait has been identified with the evolution of their complex recruitment systems (Waddington et al., 1986).

The postulated relationship between quantity of the provision mass and offspring size could be offset by the quality of the provision (Wcislo and Cane, 1996). In our study, corbicular pollen masses brought into the nest and deposited into cells by females were of the same color and consistency. Of course, other factors, including protein content (Roulston et al., 2000) and glandular secretions (reviewed in Wcislo and Cane, 1996) may affect larval food quality, and pollen color and consistency may not be accurate indicators of pollen type. A report on the makeup of the pollens collected during this study will be presented elsewhere.

Phenology of foraging

Eulaema meriana, like most bees, are diurnal, limiting their foraging activity to periods between dawn and dusk. Moreover, they specialize temporally on different resources during the day, collecting pollen and nectar from dawn to early afternoon, and mud and other construction materials between afternoon and dusk (Appendix 3). Often, a female was seen returning to the nest on the last trip of the day without anything in her corbiculae. On these occasions she would go directly to the cell being provisioned and insert her head and thorax into the cell in a manner suggesting regurgitation. From this behavior we infer that these trips were to collect nectar for cell provisioning, although the females may also have consumed some nectar as a source of energy for nighttime activities. The diel shifts in resource collection are probably governed primarily by pollen availability for provisioning the brood cells. Pollen from preferred hosts is likely to be exhausted early, so benefits go

to the early-arrivals (Linsley, 1978). Mud, on the other hand is an unlimited commodity much of the year in the rain forest where these bees nest, and can be collected at any time, as can feces and resins. Early arrival at flowers for pollen collection appears to be a common pattern for large bees in both lowland tropical (Roubik, 1989) and temperate habitats (Linsley, 1978).

E. meriana also have an amazing capacity to fly in heavy downpours, an obvious advantage for foraging during the rainy season in the lowland tropics. They are robust and hairy, two additional features that might assist them in foraging during the cooler early morning hours. Only during the morning hours were females of *Eulaema* (sp.), probably *E. meriana*, seen foraging near observation nests; they were visiting flowers of the genera *Calathea* and *Monotagma* (family Marantaceae).

Larval provisioning requires large expenditures of time and energy for *E. meriana*. The average pollen-collecting trip lasted 2 hours, and females commonly made between three and four sequential trips. Besides high costs in time and energy, this amount of time away from the nest could increase the risk of brood parasitization or removal of pollen provisions by scavengers. Although brood cells remain open until they are fully provisioned over several days, we saw few scavengers, only the occasional cockroach or small ants. If meloids, leucospids, mutillids, *Exaerete* and *Aglae* (cleptoparasites of *Eulaema*) represent the major risk to offspring (see below; also see references in Zucchi et al., 1969; Roubik, 1990), then the behavior of leaving a partially provisioned cell open while foraging adds no increased risk. Meloid triungulins come in on the bees and probably drop into the brood cell during pollen removal from the corbiculae or regurgitation. Leucospids oviposit onto a larva or pupa through the wall of the closed host cell. As for mutillids, Roubik (1990) reports that they ignore open cells while in the nest. In our study there were no instances of cleptoparasitism by *Aglae* or *Exaerete*, but they probably open recently sealed cells, replace the egg with their own and then reseal the cell (Bennett, 1972). However, we are just beginning to learn about the behavior of cleptoparasitism in *Eulaema* (Garófalo and Rozen, 2001). Further quantitative study would bring to light some of the mechanisms and risks of parasitization, and its potential role in the evolution of nesting behavior.

Nest size

Large multi-female nests are facultative in *E. meriana* (Dodson, 1966; Bennett, 1965). While most of our study nests remained small (4–5 brood cells), some were larger. For instance, the *Lizard* nest contained 14 cells, divided into two layers of 7 cells each, which was probably the product of two different females. The *Comedor* nest was the only large nest found during our study. With approximately 76 cells, this nest was probably produced by many females, constructed over several (perhaps over many) generations, as has been inferred from reports of large field-collected nests of *E. polychroma* (Nates-Parra and González, 2000), *E. cingulata* (Dodson, 1966) and *E. meriana terminata* (Bennett, 1965). It is possible of course that the *Comedor* nest was actually the product of only a few females, the two we observed and the three that were found dead in the nest. For instance, females of *E. nigrita* can construct many more than a mean of four brood cells and this varies among females (e.g., 11 cells, Pereira-Martins and Kerr, 1991; 23 cells, Santos and Garófalo, 1994).

In the small, single-female nests, each cluster of cells represents the lifetime reproductive output of one female. Many females appear to have an average reproductive capacity of four or five brood cells. This is based on our assumption that when one of our study females did not return to her nest it was usually because she had died (predation, severe

weather, senescence) rather than because she had begun a new nest elsewhere. Individual reproductive output may be greater in larger nests if females cooperate in division of tasks. However, our data are too few to draw any definite conclusions, and additional long term observations of multi-female nests are needed. Further comparative data from long term observations of large and small nests of *E. meriana* and closely related species could show how large nests develop, and ultimately reveal why eusociality has never evolved in the Euglossini, the only tribe of corbiculate bees that is not eusocial.

Facultative sociality

The few studies of nesting *Eulaema* indicate that cell construction, provisioning and oviposition are performed by a solitary nest-founding female (Zucchi et al., 1969). Communal nest associations have been reported (Dodson, 1966; Zucchi et al., 1969; Santos and Garófalo, 1994; Nates-Parra and González, 2000), but only Zucchi and colleagues and Santos and Garófalo have examined the behavior of multiple females inside the nest. To date, there is no convincing evidence of cooperation among females (Santos and Garófalo, 1994, and references therein) and no evidence of overlapping generations in the nest (Santos and Garófalo, 1994). The absence of evidence, however, is not evidence of absence and does not exclude the possibility of more complex interactions.

Data from our study suggest that *E. meriana* typically begin nests alone, and these nests remain solitary. However, our observations also suggest they may occasionally form parasocial colonies (see Michener, 2000 for discussion of social terms), containing two or more females that appear to be sisters, or at least are of the same generation. The most parsimonious explanation concerning the two females in the *Comedor* nest is that they emerged and remained in the parent nest, as did the other three females, deceased by the time we began our study. Because egg to adult development times are long for this species (100–165 days for females followed in our study; also see Roubik, 1989), mothers may not usually live long enough to overlap with daughters. Adult female lifespan, based on our study of wild nests, may not be longer than a few months; Roubik (1989) provides data attesting to a similar lifespan. Thus, the *Comedor* females were probably sisters. That they were sisters is also inferred by their similarly bright pile color and lack of wing wear.

Most multi-female colonies of *Eulaema* have been described as communal (Santos and Garófalo, 1994), with the females living together without division of labor. The question of division of labor among the two nest-sharing females of the *Comedor* nest remains speculative and awaits further research. However, in spite of few observations it is worth pointing out that during the two days in which we observed the females together in the nest, only one engaged in reproductive activity and there was only one open cell. The other female exhibited helper-like behavior, which included sealing the observation window and patching areas inside the nest with mud, and spreading mud over dead females lying on the floor of the nest. Meanwhile, the broody female collected pollen, feces and resin during the day and worked on the brood cell at night, apparently preparing for oviposition. She appeared ready to oviposit on the evening before she disappeared from the nest.

This separation of reproductive tasks between two females may have been only temporary. We have no way of knowing whether the helper-like female had previously constructed and laid eggs in her own cells, and was preparing ultimately to start a new cell, or whether she was even inseminated. Although, during the two days we observed her in the nest, she had no brood cell of her own, nor did she attend to any of the other clusters of brood cells or show any signs of beginning work on a new cell. This is contrary to our observations of the solitary foundresses; they began constructing new cells immediately

after oviposition and closure of a previous one. The apparent separation of tasks between the two *Comedor* females is consistent with a semisocial stage of sociality, even if temporary. In any case, whether occasional communal or semisocial colonies arise, colonial life in this species is facultative.

Natural enemies and scavengers

There is a tradeoff in the design of the nest. The thick, hard walls and resin lining of the cells constructed inside logs and tree trunks, or in subterranean cavities, seem highly protective against parasites and scavengers. However, because *Eulaema* are among the largest of bees, the brood cells are large, requiring substantial provisioning for the developing offspring. The cell remains open throughout the provisioning period, and is closed only after oviposition. As the female spends long periods away from the nest during foraging, her sealed brood and any exposed larval-food provisions are vulnerable to parasites and scavengers. Although nest entrances are often modified with protective mud walls and a narrow entrance hole, various parasites are able to gain access to the nest and attack the brood.

Thus far only a single identified species of meloid beetle (*Meloetyphlus fuscatus*) has been reported from *Eulaema* nests. In addition to our report on *E. meriana*, *M. fuscatus* has been reported from nests of *E. cingulata* (Dodson, 1966), *E. meriana* (subsp. *terminata*, Bennett, 1965) and *E. nigrita* (Pereira-Martins, 1991; Santos and Garófalo, 1994, see discussion of synonymy below). Unidentified meloids have been found in nests of *E. polychroma* (Roubik, 1990; Nates-Parra and González, 2000). Zucchi et al. (1969) listed Bennett's (1965) correct report of *M. fuscatus* as *M. attacephalus* Borgmeier. *M. attacephalus*, erected for a single individual from Brasil (apparently lost), was, however, synonymized under *M. fuscatus* by Selander (1965). Zucchi et al. (1969) and Nates-Parra and González (2000) mistakenly give the name *M. fuscata* instead of *M. fuscatus* to the sighting made by Dodson (1966).

All meloids, except the basal subfamily Eleticinae, appear to be hypermetamorphic (Bologna and Pinto, 2001), with several morphologically distinct larval stages in their developmental life-cycle: an egg, a triungulin (active first-instar larva), several feeding stages and a pupa. The triungulins are of two types, phoretic and nonphoretic (MacSwain, 1956; Crowson, 1981; Selander, 1985). The phoretic triungulin attaches itself to a host (often a flower visitor) with clasping legs and is carried back to its nest. The nonphoretic type has more typical walking legs and can find its own way into a nest. The species parasitizing *E. meriana* is of the phoretic type (Selander, 1965, 1985), and is therefore collected by the host during flower visitation (Erickson et al., 1976). The larvae probably feed on the provisions collected by the bees (Watmough, 1974; Pereira-Martins, 1991). As adults, *M. fuscatus* apparently do not leave the nest or feed (Selander, 1965, 1985). Several specialized adult features suggest adaptation to life inside a dark nest, including the loss of eyes and functional wings. Allometrically expanded heads support enormous jaws that enable them to chew through hard substrates within the nest, such as the thick clay walls of the brood cells. Selander (1965) suggested that the disproportionate allometry of the male head and mandibles was an adaptation for combat among males. This interesting hypothesis has never been tested.

The leucospid wasps that emerged from the *Lizard* nest are a new species. We report this as *Leucospis* n. sp., belonging to the *cayennensis*-group, of which there are only 8 described species. The new species represents the first account of a gregarious ectoparasitoid in the genus *Leucospis*, and will be described in a forthcoming paper (Grissell and Cameron, 2002).

Mutillids are larval ectoparasitoids of other insects, commonly of bees and wasps, which attack the late instar larvae or pupae (Brothers, 1989). The female pierces the cell or cocoon with her ovipositor and lays an egg on the host or cell wall (Mickel, 1928). The mutillid wasp found in the *Comedor* nest was *Hoplomutilla conspecta* Mickel. Other species of *Hoplomutilla* have been reported from nests of *Eulaema* (Roubik, 1990) and *Eufriesea* (Lenko, 1964).

To our knowledge, this is the first report of egg laying by lizards in the nests of *Eulaema*. It is not known whether they use the nest cavities of *Eulaema* in nature. It is probable that the harvested palm trees used at the Tiputini Biodiversity Station provided easy access to good shelter for the teeid eggs, but that otherwise there is no direct association with *Eulaema* nests.

Our data are too few to provide quantitative estimates of the effect of these natural enemies on *E. meriana*; hence their role in the evolution of *Eulaema* behavior awaits future study. However, we speculate that the practice of resealing old cells may have arisen as an active defense against parasites, such as mutillids, that oviposit into sealed cells. It is not known whether parasites of *E. meriana* can distinguish between the sealed cells that are empty or full, but the thick mud floors of the brood cells, through which mutillids attempt to oviposit, may be an additional factor to disguise cell contents. The construction of mud walls and narrow nest entrances at the openings of concealed nest cavities is also likely to reduce rates of parasitism. The composition of the resin lining of the brood cells of *E. meriana* is unknown, but there may be plant compounds in the resins that assist in cell defense.

Summary

We have shown that *E. meriana* is similar in various aspects of its nest architecture and behavior to other species of *Eulaema*. Similar features of the nest include a preference for nesting in closed cavities, modification of the nest entrance by construction of a wall or short tunnel, constructing brood cells of mud, feces and resin in a comb configuration, and lining the cells with resin. We know little about social interactions in this species. Sociality is, however, a facultative trait, with the majority of nests remaining small and solitary, but with occasional large nests that may have multiple females. The multi-female nests are probably communal. As reported for *E. nigrita*, *E. meriana* nests may be used by more than one generation. Also in accordance with other *Eulaema*, egg to adult development time is long (greater than three months). Foraging behavior is similar to that described for *E. nigrita*, with a diurnal periodicity in collecting different resources: long trips to collect pollen during the morning hours and short trips to collect mud, feces and resin, often in the afternoon. Brood parasitization can be quite high, at least 40% in the case of the large *Comedor* nest. Meloid beetles appear to be a frequent parasite of *Eulaema*, as are mutillids. Additionally, we found the first instance of parasitism by a gregarious *Leucospis* belonging to a new species. Whether this parasite is particular to *E. meriana*, we cannot say.

We currently have a poor understanding of the comparative behavior of most species other than *E. nigrita* and *E. meriana*. It is not clear which female traits and tendencies are similar across all the species and which are species-specific, if any. Few behavioral characters actually differentiate *E. meriana* from other studied *Eulaema*. Perhaps there is a preference for above-ground nesting, in contrast to *E. nigrita* and *E. polychroma*, which seem to prefer subterranean cavities. Further detailed study of the natural history and phylogeny of *Eulaema* will ultimately allow the testing of hypotheses concerning the evolutionary pattern of potential ecological correlates of communal and possibly semisocial behavior found in these bees.

Why have advanced social systems not evolved (there is no evidence of evolutionary loss) in this group despite the fact that their closest relatives exhibit some of the most complex social systems known in insects? Answers to this question should shed light on the historical and ecological factors that laid the foundation for social evolution in the corbiculate bees. Relevant data must derive from studies of species that manifest "primitive" but variable levels of sociality.

Acknowledgments

We thank all the funcionarios at TBS, especially Meyer Rodriguez, Ulbio Guadalupe and Enrique Llerena for help in the field; Carlos Klein and Jaime Guerra helped with the logistics of this study. We also thank the bee-team, especially Susanna Messinger, and Jim Whitfield for assistance with field observations. We are indebted to John Pinto for identification of the meloid parasites; Eric Grissell for identification of the leucospid parasitoids; Donald Manley for identification of the mutillid wasp; Helen Kennedy for identification of the plant taxa, and Jim Whitfield for providing some of the initial drawing sketches and offering useful comments on the final drawings. We thank Carlos Garófalo, Claus Rasmussen, Charles Michener and Robert Dressler for helpful comments on the manuscript. This research was supported by a National Science Foundation grant (IBN-9973447) to SAC.

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Appendix 1. Nest cell measurements of six *Eulaema meriana* nests.

Nest	Total cavity volume (cm^3)	Total # cells	# cells sealed	# cells being provisioned	Average Cell Dimensions (mm)						
					Height	Diameter		Thickness			
						top	*middle*	*cap*	*walls*	*floor*	*n*
Meyer	6,240	2	1	1	28	13	15	—	2	4	1
Susanna	17,177	4	3	1	29 ± 1.3	12 ± 0.5	17.5 ± 0.6	7.5 ± 1.1	1 ± 0.0	3.5 ± 0.6	4
Lab	3,060	1	1	0	29	15	17	11	1.5	5	1
Comedor	36,079	76	75	1	29 ± 1.4	12 ± 0.9	16 ± 0.6	6.8 ± 1.4	3 ± 0.7	7.6 ± 2.5	20
Lizard	15,835	14	13	1	28 ± 1.7	12.5 ± 1	15.75 ± 0.3	7.7 ± 2.1	2 ± 1	3	4
Enrique	3,305	4	3	1	—	—	—	—	—	—	0
mean: SD	13,616 ± 12,604	16.83 ± 29.35	16.0 ± 29.25	0.83 ± 0.40	28.60 ± 0.55	13.0 ± 1.25	16.3 ± 0.97	8.4 ± 1.8	1.9 ± 0.75	4.6 ± 1.8	

Dimensions of nest cavity	
Meyer	Attached to floor of suspended drawer under dorm approx1.5 m above ground: 4 cm high × 39 wide × 40 cm deep
Comedor	Top of palm to nest attachment 150 cm, diam. inside palm 17.5 cm, nest to bottom of palm (ground) 80 cm
Susanna	Top of palm to nest attachment 120 cm, diam. inside palm 13.5 cm, nest to bottom of palm (ground) 40 cm
Lizard	Top of palm to nest attachment 125 cm, diam. inside 12.7 cm, nest to ground 20 cm
Lab	Roof cavity width 8.5 cm, length 40 cm, height 9 cm, located 4.5 m from ground surface.
Enrique	Width between outer and inner wall of building 8.5 cm, length 24 cm, height 16.21 cm

Appendix 2. Measurements of brood cell provisions of four *Eulaema meriana* nests. Pollen refers to the pollen and nectar mixture within each cell; inc refers to an incompletely provisioned cell.

	Meyer Cell #		*Susanna* Cell #				*Enrique* Cell #				*Lab* Cell #
Nest	1	2	1	2	3	4	1	2	3	4	1
Pollen depth (mm)			12	15	13	inc	10	12	13	10	10.5
Pollen weight (g)			2.2	2.7	3.1	inc	–	–	–	–	1.9
Pollen volume (ml)			2.1	2.6	3.2	inc	–	–	–	–	1.8
Cell height (mm)	28		21	28.5	28	31	–	–	–	–	30
Cell diameter (mid)	15		18	18	17	17	–	–	–	–	17

Appendix 3. Mean foraging activity for each resource during 1-hr intervals, dawn to dusk, averaged over all observation days for Enrique and Comedor nest females. Each cell represents the total number of trips and total collecting time spent during each hour-interval

Time	Mud # trips (*time*)	Pollen	Feces	Resin	No loads
5:01–6:00					
6:01–7:00	1 (*0:03:00*)			1 (*0:32:00*)	
7:01–8:00		8 (*15:36:00*)		2 (*1:04:00*)	
8:01–9:00	9 (*0:27:00*)	2 (*3:54:00*)		1 (*0:32:00*)	
9:01–10:00	8 (*0:24:00*)	5 (*9:45:00*)			1 (*0:20:00*)
10:01–11:00	18 (*0:54:00*)	5 (*9:45:00*)			
11:01–12:00	21 (*1:03:00*)	1 (*1:57:00*)			
12:01–13:00	15 (*0:45:00*)	7 (*13:39:00*)	2 (*0:39:26*)		
13:01–14:00	13 (*0:39:00*)	3 (*5:51:00*)		2 (*1:04:00*)	2 (*0:40:00*)
14:01–15:00	31 (*1:33:00*)		4 (*1:19:00*)	3 (*1:36:00*)	
15:01–16:00	43 (*2:09:00*)		4 (*1:19:00*)	2 (*1:04:00*)	2 (*0:40:00*)
16:01–17:00	33 (*1:39:00*)		3 (*0:59:00*)	2 (*1:04:00*)	3 (*1:00:00*)
17:01–18:00	8 (*0:24:00*)				2 (*0:40:00*)