

## Nesting biology of tropical solitary and social sweat bees, *Lasioglossum (Dialictus) figueresi* Wcislo and *L. (D.) aeneiventre* (Friese) (Hymenoptera: Halictidae)

William T. Wcislo<sup>1,\*</sup>, Alvaro Wille<sup>2</sup>, and Enrique Orozco<sup>2</sup>

<sup>1</sup> Department of Entomology, University of Kansas, Lawrence, KS 66045-2119, USA

<sup>2</sup> Museo de los Insectos, Universidad de Costa Rica, Ciudad Universitaria, Costa Rica

**Key words:** *Lasioglossum*, Halictidae, social behavior, phenology, nest architecture.

### Summary

The nesting biology of a mainly solitary bee, *Lasioglossum (Dialictus) figueresi*, is compared with that of a possible relative and mainly eusocial bee, *L. (D.) aeneiventre*. These bees nest in the ground in highly disturbed areas in the Meseta Central of Costa Rica. Information is provided on social organization, male production, diel and seasonal activity patterns, pollen utilization, natural enemies and nest architecture.

*L. (D.) figueresi* nests within aggregations in vertical earthen banks, and 80–90% of females are solitary during the nest-provisioning phase. Social nests contain two (or rarely three) females which may be either equal or unequal in reproductive status (i.e. mated with developed ovaries or not). Solitary nests and two-female nests do not experience different rates of parasitism. Mid-way through the dry season, females cease provisioning at a time when other *L. (Dialictus)* remain active. Females typically remain within their nests, although they occasionally forage for nectar. This behavior is similar of that of “spring gynes” of temperate eusocial species. The egg-to-adult developmental rate of *L. (D.) figueresi* is unusually slow for halictine bees, however, so that all the adult females die before their brood eclose in April and May, precluding overlap of generations. The eclosed offspring remain in open cells within their natal nests until mid-June, when both males and females emerge to mate. These newly mated females either establish new nests or re-use old ones.

*L. (D.) aeneiventre* nests within aggregations in horizontal ground or in vertical banks. A foundress female digs a nest at the beginning of the dry season, although some re-activate old nests. Foundress nests develop into colonies with various kinds of social organization. In contrast to *L. (D.) figueresi*, *L. (D.) aeneiventre* is active nearly all year round, except during periods of heavy rain, and produces up to three broods per year.

\* Present address, and that for correspondence: Department of Entomology, Cornell University 14853, USA.

Sweat bees (Hymenoptera: Halictinae) are a socially heterogeneous group of mainly ground-nesting bees which are abundant world-wide. Intra-specific variation in social behavior is prevalent both within and among populations, presumably indicating social and environmental control of behavioral modifications (see e.g. Sakagami and Munakata, 1972; Eickwort, 1986; Packer, 1990; Yanega, 1988; reviewed in Michener, 1990). The initial stages of hymenopteran social evolution are represented by solitary individuals and those in undifferentiated societies, yet their biology is not well known, as is true for the numerous tropical halictine species or populations (see Michener, 1990).

The subgenus *Dialictus* of *Lasioglossum* is a primarily New World group of several hundred species (Moure and Hurd, 1987). These bees are monotonously similar in structure and appearance, yet diverse in social behavior. Female *Lasioglossum* (*Dialictus*) *figueresi* are usually solitary, and structurally are very similar to their social relative *L. (D.) aeneiventre* (Wcislo, 1990a). The systematic placement of these species with respect to other *L. (Dialictus)* is uncertain, but they have no obvious affinities to other recognized species groups (G. C. Eickwort, pers. comm.). Unusual morphological features, such as large size, yellowish wings and pubescence, and features of the genital organs, may indicate that *L. (D.) figueresi* is the more derived of the pair, and may therefore be secondarily solitary, as is known for other sweat bees (Packer, 1991).

### Materials and methods

Data on colony composition, social organization, and other related attributes were obtained through periodic nest excavations. Prior to being excavated, nests in horizontal ground were filled with liquid plaster of Paris which was allowed to harden; nests in vertical banks were filled with a fine powder (flour or dry plaster of Paris) blown into the tunnel. These methods enabled us to follow the tunnels through the soil. Cell contents were placed either in preservatives, or in individual chambers of wax or plastic tissue-culture trays covered with moistened filter paper, for rearing. The residents were collected and preserved in Kahle's solution for dissections and measurements of socially relevant traits (cf. Michener et al., 1958; for rationale see Michener, 1974).

Data on nest architecture were taken following Sakagami and Michener (1962); features were sometimes observed in the field with a 10X hand lens for *L. (D.) figueresi*, or later examined in the laboratory using a stereomicroscope. Nearest-neighbor distances (NND, Clark and Evans, 1954) between nests were recorded in the field with a mm ruler [*L. (D.) figueresi*], or determined from maps of the nest site [*L. (D.) aeneiventre* for *Area cafetal*].

Adult body size (head width, and for some specimens, length of right forewing) was measured with an ocular micrometer in a stereomicroscope. Females were dissected to examine and measure ovarian development (length and width of the largest developing oocyte). Any evidence of resorbed oocytes was noted for *L. (D.) figueresi*, but not for *L. (D.) aeneiventre*. For the latter, this measure of ovarian development may be biased against females which had recently laid or resorbed eggs,

and biased for larger females, or those with only one well-developed ovariole. Spermathecae were removed, squashed between a clean glass slide and coverslip, and examined under a compound microscope for the presence of a clump of spermatozoa. Adult males and females [*L. (D.) figueresi*] were dried in an oven to a constant weight, which was determined using a Mettler® electronic balance.

An estimate of the amount of nest-constructing work done by individuals was obtained by determining the degree of mandibular wear, using indices of Michener and Wille (1961). Wing wear was estimated by counting the numbers of nicks on the edges of the forewings; unworn bees were presumed to be young, recently emerged bees.

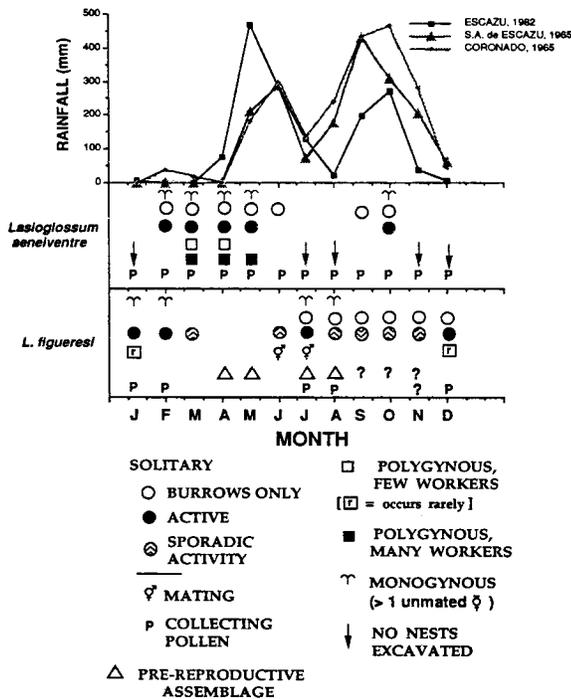
Data on provisioning behavior were obtained by observing bees individually marked on the thorax with paint, and durations of activities were timed with a watch to the nearest second.

Statistical methods are indicated in the text, and were taken from Sokal and Rohlf (1981) and Conover (1971), or from Statworks® and Statview® on a Macintosh SE® computer. Means are given with their standard errors unless otherwise indicated (SD = standard deviation).

The study sites were in highly disturbed, heavily populated and intensely cultivated areas near San José, San José Province, Costa Rica. In these semi-rural areas there are many trails and earthen roads cut through hillsides, creating extensive stretches of substrate for ground-nesting bees and wasps (Fig. 1). San Antonio de Coronado and San Antonio de Escazú overlook the capital city of San José, facing each other from opposite slopes of the Cordillera Central, northeast and southwest, respectively, nearly 20 km apart. The climate and seasonal phenology of plants seemed similar on both slopes; in general, San Antonio de Coronado is slightly cooler and wetter than San Antonio de Escazú. The dry season begins in late November or December, and lasts until April or May, when rains begin. The rainy season continues



**Figure 1.** Nest-site of *Lasioglossum figueresi* (San Antonio de Escazú, Costa Rica). In the earthen bank between the foreground and the insect net were nests of > 300 bees. The insect net is approx. 1.3 m tall



**Figure 2.** Nesting phenologies and social organization of *Lasioglossum figueresi* and *L. aeneiventre*, along with seasonal precipitation in Escazú and Coronado, Costa Rica (from Anonymous 1965, 1982). Symbols: OPEN CIRCLE = nest tunnels with no cells; CLOSED CIRCLE = active nests with cells, each with one adult female; SHADED CIRCLE = nests which are intermittently active during favorable weather, each with one adult female; OPEN SQUARE = nests with > 1 mated female, and < 3 unmated workers; OPEN SQUARE + r = as above, but rare; CLOSED SQUARE = nests with > 1 mated female and > 3 unmated workers; WING = nests with one mated female and ≥ 1 unmated worker(s); TRIANGLE = nests with recently emerged (unworn), unmated adults which cohabit a nest during an unfavorable period; P = females observed entering nests with pollen; ↓ = no nests were excavated; ♀ = adult males present, and mating

to November, broken by a brief period (*veranillo*) of reduced rainfall (Fig. 2; also Coen, 1982).

*L. (Dialictus) figueresi* usually nests in aggregations, which are abundant at higher elevations (> 1200 m) in mixed residential-agricultural areas throughout the Cerros de Escazú [see Wcislo (1991) for its known range]. The majority of the observations were made at the following sites near San Antonio de Escazú:

- a) *Near site* (Fig. 1): Several hundred bees nested in a west-facing vertical earthen bank of a road passing through land cultivated with mixed crops at about 1450 m elevation. A very old local farmer stated that bees had been nesting at this site for many years.
- b) *Station 9*: Bees nested in a north-facing vertical earthen bank on the first side trail about 300 m south of the religious shrine "IX ESTACION Jesus Cae por Tercera Vez" on the way to La Cruz del Alajuelita, which is on the summit of Cerro San Miguel. This aggregation (elevation approx. 1600 m) is approximately 1.5 km

southeast of *Near site*, and is surrounded by coffee trees and open pasture. This site is heavily shaded by cypress evergreen trees (Cupressaceae). In 1985 this aggregation was thriving (> 300 active nests), yet by 1988 it was nearly extinct (2 active nests out of 35 rapidly excavated nests; the remainder were obviously old, abandoned nests). The vegetation had become much thicker, and it seems likely that the site had become less suitable because of the decreased sunlight.

- c) *Nice view*: Bees nested in both east- and west-facing banks (elevation approx 1700 m) on a trail approximately 3 km due south (uphill) of a school-house, Escuela Carmen, which is several kilometers southwest of San Antonio de Escazú. The area surrounding this site is open pasture, with pockets of forest on the steeper slopes and bordering trails.

Observations and nest excavations on *L. (D.) figueresi* were made by WTW 2–3 times each week while bees were flying, and weekly or bi-weekly when they were not actively provisioning, for most weeks from 15 January to 20 April 1986 (23 day-long visits), 14 December 1986 to 28 May 1987 (40 visits), 10 December 1987 to 16 January 1988 (22 visits), and 30 May to 2 August 1988 (20 visits). At irregular intervals from May to November 1986, Marla Spivak briefly observed the bees and excavated several nests.

Three aggregations of *L. (D.) aeneiventre* were observed on a farm approximately 1 km west of San Antonio de Coronado, San José Province (9°59'N, 84°00'W, elevation approx. 1380 m), and a fourth site was located approximately two kilometers from the others:

- a) *Area Cafetal*: Bees nested in an aggregation in flat to gently sloping (< 10°) ground with sparse to no surface vegetation within a clearing in a field of coffee (*Cafe*) plants.
- b) *Area Casa*: Bees nested in an aggregation in flat to gently sloping ground in an area free of vegetation near a house. This site was approximately 100 m from *Area cafetal*.
- c) *Area Desagüe*: Bees nested in flat or sloping (approx. 45°) ground near a drainage ditch in a field.
- d) *Iglesia*: Bees nested in a 1 m × 3 m section of a nearly vertical earthen, south-facing and fully-exposed bank along the drainage ditch beside a paved road in a residential area, approximately 3 km south of the Iglesia de San Isidro de Coronado (elevation approx. 1300 m). The bank was sparsely covered with grasses, dandelions and lichens. These observations show for *L. (D.) aeneiventre* the lack of a strict requirement for substrate orientation, as known for some halictine bees (Sakagami and Michener, 1962).

Observations and nest excavations of *L. (D.) aeneiventre* were made at the *Casa*, *Cafetal*, and *Desagüe* sites by AW and EO in March, April, June, and October 1970, October 1982, and February, April, and May, 1983, with brief visits at various other times. In December, 1985, EO and WTW visited these sites without finding any nesting bees. WTW made some brief observations (approx. 10 hours total over 7 days) at the *Iglesia* site in December, 1985, before it was destroyed by road construction.

Voucher specimens of *L. (D.) figueresi*, associated parasites, cells, turrets, soil and pollen samples are in the Snow Entomological Museum, University of Kansas (KU); additional bee vouchers are in the Instituto Nacional de Biodiversidad (Santa Domingo, Costa Rica) and elsewhere (Wcislo 1990a). Specimens of *L. (D.) aeneiventre* with "Coronado" locality data (collected: A. Wille) are also in the KU collection, as are *L. (D.) aeneiventre* specimens from the population studied by WTW.

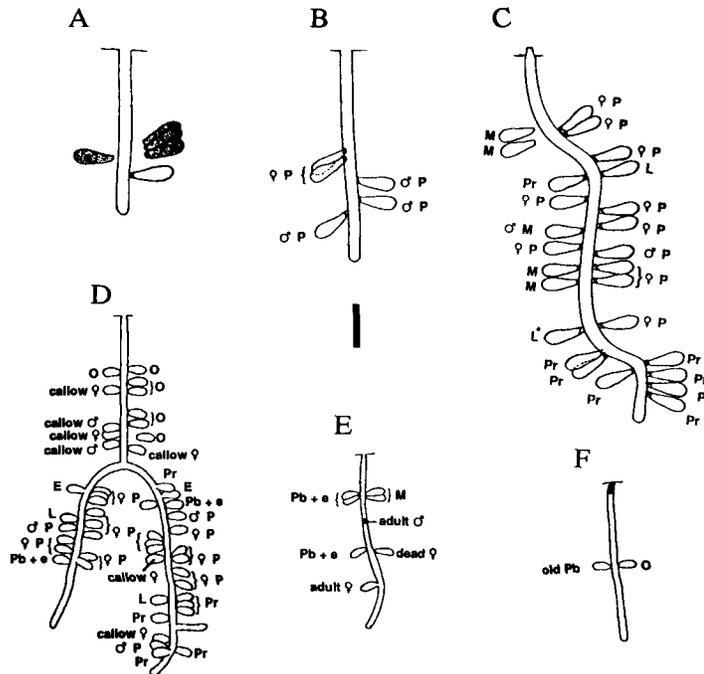
## Results

### *Lasioglossum (Dialictus) figueresi*

*Nests:* Females usually nested within aggregations, although rarely isolated nests were found from 50 m to several kilometers from the nearest aggregation. Nests were clustered within aggregations, such that sometimes two or three active nest entrances were actually fused to one another. Nests were, on average, separated from their neighbors by about half the distance expected under randomness ( $R = 0.5$ ,  $r_A = 6.9$ ,  $c = 2$ ,  $n = 58$ ,  $0.01 < P < 0.05$ ) [Clark and Evans (1954); Simberloff's (1979) correction was not necessary since the nest entrance diameter ( $\sim 0.5$  cm) was much smaller than  $\{1/2$  (expected mean NND)}; Sinclair (1985) states that the Clark and Evans' statistic may not be valid for sample sizes smaller than 100].

Nests were conspicuous owing to the 4 mm to 28 mm ( $\bar{x} = 6.4 \pm 4.1$  mm,  $n = 42$ ) earthen turrets usually projecting from the entrances on the vertical bank. Nest architectural features otherwise did not differ in qualitative ways from those of other *L. (Dialictus)*, and are classified as subtype III b of Sakagami and Michener (1962) (Fig. 3a–c). Turret entrances were constricted, having inner diameters from 2.7 to 3.4 mm ( $\bar{x} = 3.0 \pm 0.3$  mm,  $n = 42$ ); the outer diameters ranged from 4.1 to 6.0 mm ( $\bar{x} = 5.2 \pm 0.5$ ,  $n = 42$ ). Each turret consisted of numerous small balls of mud, visible as rough bumps on the exterior surface. The inner surface was smoothed but no polished, and there were no obvious signs of secretions such as can be seen in the cell linings or turret linings of some halictids (refs. in Wcislo, in press a). Turrets were constructed at night during the beginning of the active season. Females carried soil from within the nest, and then tamped it into place with their pygidia. Turrets were sometimes replaced or repaired if damaged, but only when the soil was still moist and malleable [see Hicks (1931) for similar behavior in another halictid]. Females did not add a constriction to the burrow entrance after a turret had been removed or was damaged, unlike some halictine bees (Sakagami and Michener, 1962).

Beyond the surface of the bank, the nest tunnel diameter ranged from 4.1 to 6.0 mm ( $\bar{x} = 5.2 \pm 0.05$ ,  $n = 42$ ), and did not change as the tunnel went deeper into the bank. The first cells were 2 to 11 cm beyond the surface at three sites, based on nests excavated in February, 1986 [*Near*:  $\bar{x} = 5.1$  cm  $\pm$  0.68,  $n = 12$ ; *Station 9*:  $\bar{x} = 5.9 \pm 0.84$ ,  $n = 12$ ; *Nice*:  $\bar{x} = 5.5 \pm 0.68$ ,  $n = 12$ ]. Nest tunnels were approximately perpendicular to the bank surface, or slightly sloped downward with some meandering. Nests extended up to 24 cm into the bank. Mean maximum tunnel depth at *Near* was 11.9 cm  $\pm$  1.53 ( $n = 12$ ); *Station 9*:  $\bar{x} = 15.4 \pm 1.33$  ( $n = 12$ ); and *Nice*:  $\bar{x} = 16.4 \pm 1.5$  ( $n = 12$ ).



**Figure 3.** Schematic drawings of representative nests of *Lasioglossum figueresi* (a-c; scale bar = 1.5 cm), and *L. aeneiventre* (d-f; scale bar = 2.5 cm). E = empty cell; Pb + e = pollen ball with egg; L = larva; Pr = prepupa; P = pupa; M = cell with mold; O = old cell filled with soil; shaded cells are from a previous year and may not be associated with that nest

Cells had the usual shape for those of Halictini, and were 9 to 13 mm long ( $\bar{x} = 10.1 \pm 0.49$ ,  $n = 10$ ), 4 to 6.5 mm in diameter at the widest part ( $\bar{x} = 5.8 \pm 0.34$ ,  $n = 10$ ), tapering to 2 to 3.6 mm at the collar ( $\bar{x} = 2.9 \pm 0.2$ ,  $n = 10$ ), and were lined with a thin, shiny secretion. Plugs consisted of 1 to 4 mm ( $\bar{x} = 1.8 \pm 0.34$ ,  $n = 10$ ) of packed soil. Usually cells were joined to the main tunnel with very short (< 2 mm) lateral tunnels, although rarely there were lateral tunnels up to 10 mm long, which were filled in with packed soil. The long axes of cells sloped slightly (<  $10^\circ$ ) downward from the entrances. Old cells with feces usually were not re-used, and were often partially or completely filled with soil. Feces were deposited by the larva on the upper rear wall of the cell. In two of more than 647 cases a cell contained both old dried feces and a fresh, partially eaten pollen ball and a larva, showing that it was re-used. Between one and five empty cells were built early in a nest's ontogeny, unlike many halictines, so that very young nests had up to several open, empty cells; older nests likewise contained open, empty cells.

**Seasonal Cycle:** The majority of nests were occupied by a single female and her immature offspring (below). A schematic representation of the life-cycle is given in Figure 2. During a brief period of reduced rainfall (late June to early July) females emerged from their nests, mated, and then established nests. Most females

established new nests, while the others (< 10%) re-used old nests, judging by the presence of old cells with their nests. Some females sporadically provisioned a few cells during brief periods of favorable weather in July through September, but during October and much of November the heavy rains resulted in the cessation of activity. At the start of the dry season in late November to early December, females began to extend nest tunnels and construct cells. Bees provisioned cells with pollen until mid-February when provisioning ceased. After this time the adult females did not leave nests to forage for pollen. Similar behavior is reported for many spring foundresses of seasonally active eusocial halictids (see Discussion). *L. (D.) figueresi* adult females, however, died without further reproduction. No marked bees (n = 143) were recovered in a second year. Additionally, all nests excavated at the beginning of the dry season contained bees with unworn wings, while nests excavated during late February typically contained adult females with worn wings and mandibles, and those excavated after this time were increasingly likely to contain dead, dried females.

Broods developed continuously throughout the provisioning phase, and continued to do so until the end of April when young eclosed in the nest as callow adults (Fig. 4). As the dry season progressed, the soil became drier and harder, and it was probably difficult for bees to establish nests. Young adults remained in their natal nests until mid-June, when both males and females emerge and mate (details in Wcislo, 1992). Callow females taken from various nests in April and May did not have sperm in their spermathecae (n = 10).

*Larval development:* Durations of developmental stages for *L. (D.) figueresi* are given in Figure 4 for *Near site*. [Immature stages were not successfully reared in the laboratory]. Extrapolating from these data, the estimated total duration for development from egg to adult is approx. 80 days, longer than in other halictine bees (reviewed in Wcislo, 1991). Similar developmental stages were found in nests at various aggregations at the same time of year, with a slight lag of 4–5 days for aggregations at higher elevations.

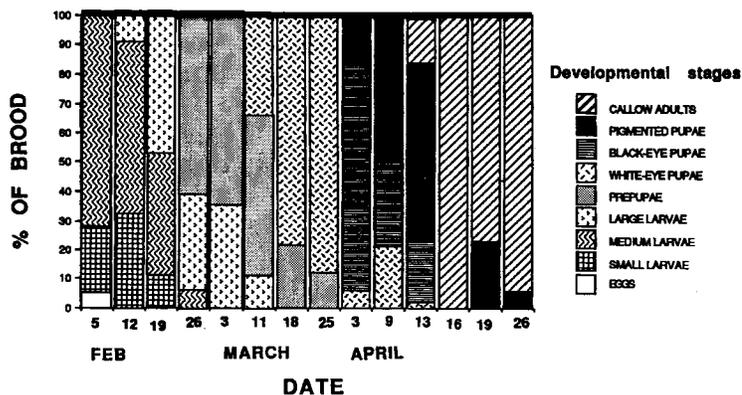


Figure 4. Population summary of developmental stages of brood of *Lasioglossum figueresi* from *Near Site* (1986). Each sample period is based on excavations of 6 to 10 nests

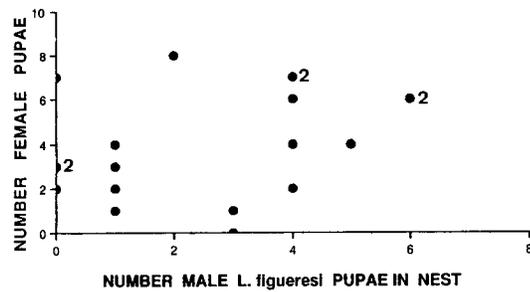


Figure 5. Scatter plot of the number of male pupae versus the number of female pupae in nests of *Lasioglossum figueresi* at *Near site* from 1986. Each point represents one nest unless indicated otherwise

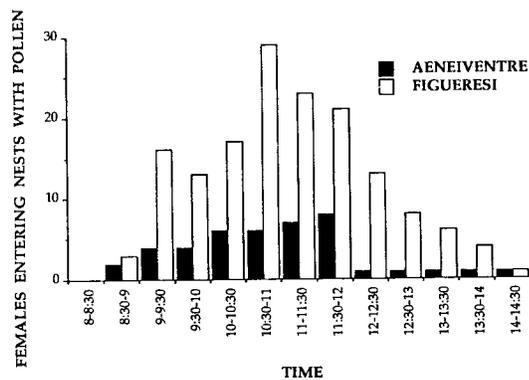
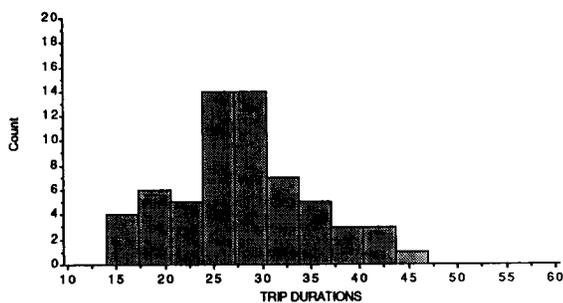


Figure 6. Diel provisioning activity of *Lasioglossum figueresi* (*Near site*, Jan., Feb. 1986,  $n = 10$  nests) and *L. aeneiventre* (*Area Desagüe*, April 1983,  $n = 7$  nests)

Data on pupal sex ratio are given in Figure 5. The number of female pupae per nest ranged from 0 to 8 [ $\bar{x} = 2.8 \pm 0.48$ ,  $n = 25$  nests], and the number of male pupae ranged from 0 to 6 [ $\bar{x} = 2.2 \pm 0.34$ ,  $n = 25$ ] ( $P > 0.4$ , Mann Whitney U test). The mean sex ratio (male pupae/total pupae) was 0.48 ( $SE = 0.06$ ). The mean dry weight of adult females ( $\bar{x} = 7.25 \text{ mg} \pm 0.84$ ,  $n = 8$ ) was slightly greater than that of males ( $\bar{x} = 5.41 \pm 0.5$ ,  $n = 12$ ) ( $P = 0.06$ ,  $t = -2.00$ ).

*Diel activity:* Females began foraging between 8:00 and 9:00, or generally when the air temperatures exceeded 20 to 21 °C. Bees often sat for long periods of time at the nest entrances (up to 14 minutes) before leaving the nest to forage, and early in the morning were commonly observed half-way out of the nest, presumably warming up flight muscles. A histogram of diel provisioning behavior is given in Figure 6 for bees at *Near site* (pollen trip durations pooled over January and February, 1986), along with data for *L. (D.) aeneiventre*. Foraging trip durations ranged from 7 to 46 minutes [ $\bar{x} = 28.4 \pm 0.9$ ,  $n = 62$ ], and bees usually made 1 to 5 trips per day when the weather was favorable (Figure 7: data from January, 1987).



**Figure 7.** Distributions of the durations of pollen-gathering foraging trips by female *Lasioglossum figueresi* (Near site, Jan. 1987)

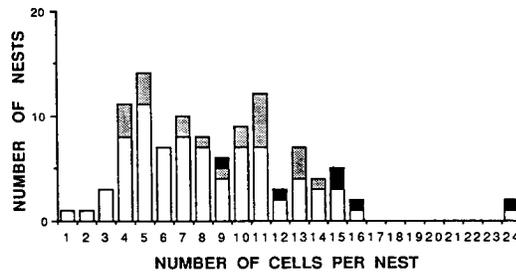
**Table 1.** Percentages of multi-female nests of *Lasioglossum figueresi* during the active provisioning phase. The number of nests per sample is given in parentheses. Nests with unknown or uncertain numbers of females were excluded. Roman numerals indicate months

Dates	Percentages of nests with two females		
	Near site	Station 9	Nice view
I-V, 1985	16(25)	14(7)	-
I-IV, 1986	21(28)	20(5)	-
XII, 1987-I, 1988	19(16)	20(5)	26(15)
VI-VII, 1988	9(21)	-	13(15)

Pollen balls ranged from 15.0 to 48.5 mg (dry weight after drying to a constant weight at 50 °C) ( $\bar{x} = 30.7 \pm 2.94$ ,  $n = 12$ ). Pollen from pollen balls consisted mainly of *Melampodium divaricatum* (Asteraceae), as well as *Croton bilbergianus* (Euphorbiaceae), *Solanum?* (Solanaceae), and an unknown Asteraceae sp. (D. Roubik, *in litt.*); another sample contained pollen from at least two different kinds of Asteraceae. *L. (D.) figueresi* represents the first record of a halictid bee using *Melampodium* pollen (Moure and Hurd, 1987).

**Social organization:** Most females were solitary. Adult females were unimodal in size, with a mean headwidth of  $2.3 \pm 0.01$  ( $n = 93$ ,  $CV = 4.2$ ), and there were no significant seasonal (monthly) size differences among *Near site* females throughout the year [ANOVA:  $F_{(7,109)} = 0.911$ ,  $P > 0.25$ ; sizes pooled for May and June, September to November, and December and January].

The percentages of nests with 2 females during the provisioning phase for various years ranged from 9 to 21% (Tab. 1), and did not differ significantly between years or localities. Fewer two-female nests, however, were found in August. Solitary bees [ $\bar{x}$  headwidth =  $2.4 \pm 0.05$ ,  $n = 20$ ] were not larger than females from two-female nests [ $\bar{x} = 2.32 \pm 0.03$ ,  $n = 14$ ]. Among the latter, mated females ( $\bar{x} = 2.3 \pm 0.04$ ,  $n = 11$ ) were the same size as unmated ones ( $\bar{x} = 2.36 \pm 0.07$ ,  $n = 3$ ). The spermathecae of both females were examined in 7 two-female nests: in 4 pairs both females were mated and had well-developed ovarioles, and in 3 pairs one female



**Figure 8.** The number of cells per nest for *Lasioglossum figueresi* nests at *Near site* with one (shaded bars), two (black bars) or an unknown number of females (white bars) [from 1986]

was mated with developed ovarioles and one was unmated with undeveloped ovarioles.

Based on mature nests excavated after provisioning had ceased in February, 1986, the number of cells per nest for single-female nests ranged from 0 to 14 [ $\bar{x} = 8.9 \pm 0.69$ ,  $n = 24$ , *Near site*], while nests known to have 2 females contained up to 24 cells [ $\bar{x} = 11.6 \pm 3.36$ ,  $n = 6$ ] (Wilcoxon two-sample test,  $U_5 = 105.5$ ,  $0.01 > p > 0.002$ ) (Fig. 8).

*Natural enemies or associates:* The principal natural enemy of *L. (D.) figueresi* at all aggregations was the fly *Phalacrotophora halictorum* (Melander & Brues) (Diptera: Phoridae). Details of the parasitic behavior of this fly are given in Weislo (1990b). Many nest cells contained fungi, but it was impossible to determine whether a fungus was the agent of morbidity or whether it represented a secondary invasion. Based on mature nests with known numbers of adult females, single-female nests had a mean of 21% of all cell contents destroyed ( $SE = 0.04$ ,  $n = 34$  nests). In comparison, two-female nests had 20% of their cells destroyed ( $SE = 0.04$ ,  $n = 8$ ) (pooled from mid-February to April, 1985–1987; Wilcoxon two-sample test, n.s.).

#### *Lasioglossum (Dialictus) aeneiventre*

*Nests:* Female *L. (D.) aeneiventre* nested mainly in horizontal ground, but occasionally did so in vertical banks. Nests were observed clumped together in aggregations, but within one aggregation (*Area Cafetal*) the distribution of nests did not differ significantly from random ( $r_A = 19.71$ ,  $R = 0.9$ ,  $c = 0.87$ ,  $n = 21$  nests,  $P > 0.5$ ).

The entrances to active nests on flat ground were frequently surrounded by a symmetrical mound of earth (tumulus) piled around each entrance. These tumuli were usually washed away after rains, and the nest entrance constrictions were then repaired. On horizontal ground nests entered the soil at a  $90^\circ$  angle, and continued downward, with usually only slight meandering. Mature nests sometimes contained branches of the main tunnel, beginning at 12 to 20 cm depth (Figure 3d–f). Cells were found beginning at 4 cm below the surface (Tab. 2). Features of nest architecture did

**Table 2.** Summary of nest characteristics of *Lasioglossum aeneiventre*. Means are given with standard deviations. The number of excavated nests per sample is given in brackets (data pooled over the *Cafetal*, *Casa*, and *Desagüe* aggregations)

Date [nests]	Total Cells	New Cells	Old Cells	Nest Depth (cm)
February [13]	8.0 ± 4.1	1.2 ± 0.8	3.2 ± 2.0	10.0 ± 3.1
March [19]	23.6 ± 16.7	1.2 ± 1.5	5.2 ± 4.5	18.1 ± 9.8
April [32]	20.3 ± 21.7	0.7 ± 0.9	5.5 ± 8.2	16.5 ± 7.0
May [21]	5.3 ± 9.6	0.09 ± 0.3	3.7 ± 7.8	12.3 ± 5.6
June [6]	6.5 ± 7.3	0.6 ± 0.9	5.2 ± 5.7	18.1 ± 7.7
October [6]	1.2 ± 1.5	0.2 ± 0.5	0.2 ± 0.5	7.7 ± 2.5

not differ appreciably from those of other *L. (Dialictus)*, and also were subtype III b of Sakagami and Michener (1962). Cells had the usual halictine shape, 9 to 11 mm long, 3 to 4 mm in diameter at the widest part, and tapered to 2 mm at the collar which was sealed with a 2 mm plug. Cells were connected to the main tunnel without lateral tunnels. Old cells were apparently not re-used, since old cells with feces were filled with soil, while others were plugged. At least young nests in vertical banks were similar to those described above, except that they lacked tumuli. Nest tunnels were perpendicular to the vertical bank, and extended 10 to 18 cm into the bank.

Pollen was mixed with nectar and formed into a pollen loaf (approx. 3 × 4 × 3 mm), and loaves had a unimodal size distribution (see Weislo, 1991). In multi-female nests the cells were cooperatively provisioned, since returning foragers marked with different colors of powder deposited the different powders into the same cell.

*Seasonal cycle:* Many nests were eusocial and had up to three broods per year. These bees were active nearly all year round, except for October and November when strong rains resulted in nests being temporarily closed (Fig. 2).

Recently active nests with a single female each were abundant at the beginning of the dry season (late November to December). Foundresses had mainly unworn wings and mandibles, and their nests were typically short tunnels with few or no cells (Tab. 2). Some nests with single females were re-activated from the previous season as shown by the nests having cells with dried fecal matter (3 of 6 nests in October; 11 of 13 nests in February, before brood began to emerge). In the re-activated multi-female nests there was usually one female with excessively worn wings, while the other female(s) had mainly unworn wings (5 of 6 nests in February). The very worn females were evidently survivors from the previous generation. Nests were gradually enlarged until they contained up to 66 cells and 14 females by the end of the dry season in May (Tab. 3).

A small number of new nests was established throughout the dry season (Fig. 9) by unworn, presumably recently emerged, bees. Newly established nests were again abundant from April to June (Fig. 9), and followed a cycle similar to that described above for the first generation. The female brood produced from these nests emerged in September and became mated foundresses. In September and October, 5 of 8 nests

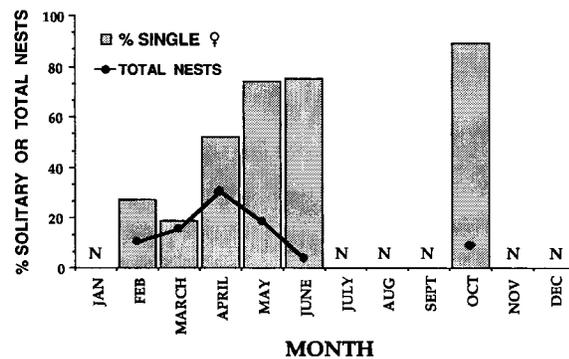
**Table 3.** Seasonal variation in total numbers of female *Lasioglossum aeneiventre* per nest for all nests, and for multi-female nests only (pooled over the *Casa*, *Cafetal*, and *Desagüe* sites). For multi-female nests their percentages of mated females per nest is given both for all bees in the nest, and excluding unworn, younger bees. Means are given with standard deviations. Sample sizes: Feb., n = 3; March, n = 19; April, n = 32; May, n = 21; June, n = 6; Oct., n = 8

Month	Females/nest (All nests)	Females/nest (Multi-female nests only)	% Mated Females/nest (all bees)	% Mated Females/nest (worn bees)
February	2.7 ± 1.1	3.1 ± 0.94	47 ± 32	68 ± 45
March	4.1 ± 3.4	5.9 ± 2.8	68 ± 33	78 ± 26
April	3.3 ± 3.8	5.8 ± 3.5	56 ± 40	74 ± 32
May	1.6 ± 1.8	4.0 ± 2.3	50 ± 49	60 ± 58
June	1.3 ± 0.6	2.5 ± 0.7	65 ± 49	65 ± 49
October	1.0 ± 0	—	—	—

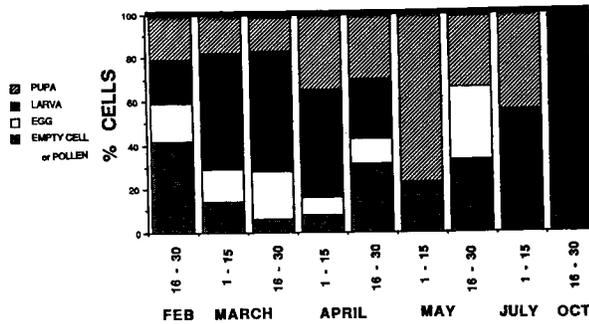
consisted only of tunnels, and the others contained few (< 3) cells. During these months females were largely inactive, although they collected pollen and provisioned cells during infrequent brief periods of favorable weather. These females probably survived until January. Their offspring emerged and either initiated new nests at the start of the dry season, or became workers or replacement queens.

*Larval and colony development:* The seasonal development of colonies is given in Figure 10. Newly constructed empty cells, as well as those with pollen balls and eggs, were found at all times throughout the year when observations were made. On the basis of periodic nest excavations, coupled with rearing in the laboratory, the total duration of egg-to-adult development was found to be approx. 35 days [durations of individual life history stages are given in Wcislo (1991)].

Males were found throughout the active cycle. Male pupae were present in the first brood to emerge in late February, and were observed in nests whenever female pupae were collected. The seasonal abundance of adult males was not quantified,



**Figure 9.** Seasonal variation in the total number of nests (circles) and the proportion of solitary nests (bars) of *Lasioglossum aeneiventre*, based on nest excavations. N = no samples were taken. Data pooled for the *Casa*, *Cafetal*, and *Desagüe* aggregations



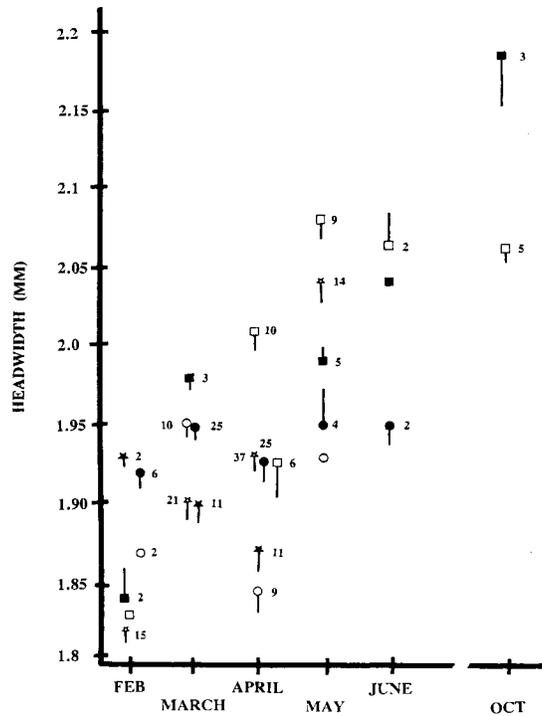
**Figure 10.** Population-level summary of seasonal changes in developmental stages of brood of *Lasiglossum aeneiventre*. Each period is based on 6 to 16 nests

although they seemed more abundant in April. Throughout the year roughly half of the females in a nest, on average, were mated (Tab. 3), suggesting that at least some males were present at all times when females were active.

**Diel activity:** Diel foraging activity of females began between 7:30 and 8:00 on clear or partly cloudy days, and continued until 14:30 or 15:00 (Figure 6). In general, flight activity began when the air temperature exceeded 18 °C. During periods of inclement weather (rain or very low misty clouds), the bees were not active outside the nest. Bees departing from the nest often lingered for long periods, partly out of the entrances, presumably warming up, as did *L. (D.) figueresi*. The pollen that bees used was not identified, although at least two colors of pollen were recorded, suggesting that these bees use a variety of floral resources, as do other *Lasiglossum* (Moure and Hurd, 1987).

**Social organization:** Levels of social organization varied among nests and within seasons. The most complex social organization was "primitively eusocial" (*sensu* Michener, 1974), but many life-history details need further study. Nests founded by single females at the beginning of the dry season produced offspring which emerged throughout late January and February. Some of these offspring remained in the nest, did or did not mate, and became workers, replacement queens or auxiliary queens. Other females left their natal nests to initiate new nests as foundresses. The proportion of solitary nests increased throughout the dry season (Figure 9), but small sample sizes in June and October preclude statistical analyses. Thirty-five of 47 solitary foundresses had sperm in their spermathecae and oocytes beginning to develop.

For a study of seasonal and caste differences in size, females with tattered wings and those with unworn wings were grouped as solitary, group-living and mated or group-living and unmated (Fig. 11). Solitary females were larger (headwidth:  $\bar{x} = 2.02 \pm 0.13$  mm,  $n = 43$ ) than females in multi-female nests ( $P < 0.0001$ ,  $t = 4.36$ ,  $df = 232$ ), regardless of whether the later were mated (headwidth:  $\bar{x} = 1.93 \pm 0.12$  mm,  $n = 85$ ) or unmated ( $\bar{x} = 1.92 \pm 0.13$ ,  $n = 109$ ) ( $P > 0.5$ ,  $t = 0.603$ ,  $df = 196$ ). This result may reflect the fact that the majority of solitary

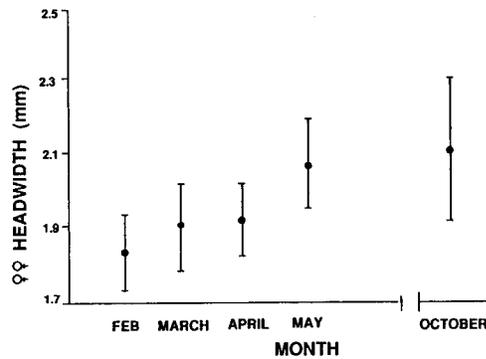


**Figure 11.** Seasonal variation in mean (+ SD) headwidth for *Lasiglossum aeneiventre* females. Symbols: OPEN STAR = unworn wings, unmated, multi-female nest; CLOSED STAR = worn wings, unmated, multi-female nest; OPEN CIRCLE = unworn wings, mated, multi-female nest; CLOSED CIRCLE = worn wings, mated, multi-female nest; OPEN SQUARE = unworn wings, solitary nest; CLOSED SQUARE = worn wings, solitary nest. Numbers adjacent to symbols indicate sample size for that point; symbols without numbers are based on a single individual

females were taken in April and May. Within multi-female nests, mated females were not larger than unmated females.

There was no positive relationship between body size and degree of ovarian development. In multifemale nests with dissection data for all occupants, the female with the most developed ovaries was the largest bee in 6 nests, tied for the largest in 4 nests, and was smaller than at least one nest-mate in 15 nests. Large solitary females each first produced a brood of smaller females. As seen in Figure 12 (unmated and unworn bees only), the size of the offspring did not change significantly until late April and May when the emerging females were as large as the solitary females, including those taken in October. Similar seasonal size variation is known in temperate species of eusocial halictids (reviewed in Michener, 1990).

The number of females per nest (pooled from all sample dates) ranged from 0 to 14 ( $\bar{x} = 2.68 \pm 0.3$ ,  $n = 99$ ), and the number of cells per nest ranged from 0 to 81 ( $\bar{x} = 13.5 \pm 1.74$ ) (Tables 2 and 3). Nests with more females had more total cells (Spearman's  $r = 0.77$ ,  $P < 0.0001$ ,  $n = 99$ ; one-tailed test for positive correlations, Conover, 1971). After excluding old cells with feces, the correlation between the



**Figure 12.** Seasonal variation in mean ( $\pm$  SE) headwidth of unmated female *Lasioglossum aeneiventre* with unworn wings (pooled from solitary and multi-female nests); none of the means are significantly different. Sample sizes: Feb.,  $n = 14$  females; March,  $n = 17$ ; April,  $n = 30$ ; May,  $n = 7$ ; Oct.,  $n = 3$

number of *active cells per female* and the number of females in the nest also was significant ( $r = 0.49$ ,  $P < 0.001$ ,  $n = 99$ ; one-tailed test for positive correlations), suggesting that groups might be slightly more efficient at building and provisioning cells than solitary females.

*Natural enemies:* Natural enemies were incidentally studied. Of 930 active cells, 4.5% (42 cells in 21 of 97 nests) were destroyed by (usually) unspecified morbidity factors. During nest excavations fly larvae (Diptera) were occasionally recovered from cells, and one cell contained nematodes. One larva was found internally in an adult bee and was probably Conopidae; two other adult females were parasitized by Strepsiptera. Female and male parasitic flies, *Phalacrotophora* sp. (Diptera: Phoridae), flew at the *Iglesia* nest site, but they were not abundant, and no immature stages were recovered from nest cells. In 6 cases (in June and October), marked female *L. (D.) aeneiventre* entered nests which were being used by conspecifics, usurped the nests, and were later seen entering the stolen nests with pollen.

## Discussion

Most traits related to social organization show a high degree of behavioral uniformity between *L. (D.) figueresi* and *L. (D.) aeneiventre*, except for a few unusual features. These features are discussed below as they relate to the possible advantages and disadvantages associated with group living.

Features of nest architecture are similar for these two species, and are generally not different from other *Lasioglossum (Dialictus)* (Sakagami and Michener, 1962). *L. (D.) figueresi* females construct nest turrets, sometimes re-use old cells, and dig  $> 1$  cell early in the season before use. Such features are absent in *L. (D.) aeneiventre*, and are rare in other *L. (Dialictus)* and Halictinae (e.g. Michener and Lange, 1958; Michener and Seabra, 1959; Sakagami and Michener, 1962; Sakagami and Moure,

1967). The excavation of several cells early in a nest's ontogeny may be associated with increasing soil hardness as the nesting season progresses, and empty cells might effectively decrease rates of parasitism (cf. Tepedino et al., 1979). For both species, cells are usually connected to the main tunnels without lateral tunnels. By comparison, a secondarily solitary *Halictus* has apparently revolved long lateral tunnels (see Eickwort and Kukuk, 1990).

The social organization varies among nests for both species. Most *L. figueresi* females are solitary bees, are mated, and have developed ovaries. In contrast, the social organization of *L. aeneiventre* includes solitary foundress nests, monogynous nests with a variable number of workers, and both large and small polygynous nests. There are no discernible ecological correlates of various levels of social organization within populations, as follows. For the mostly solitary *L. (D.) figueresi* the mean number of provisioned cells per female for solitary females was not significantly different from the *per capita* production in two-female nests. In other primitively social insects the *per capita* productivity declines with increasing numbers of females in nests (see Michener, 1964; Wenzel and Pickering, 1991). Rates of parasitism were the same for solitary and two-female nests. Energetic savings relating to nest excavations are probably not substantial, since cells and new nest tunnels are dug only when the soil is moist and readily workable.

A smaller proportion (approx. 5%) of the offspring of the social species, *L. (D.) aeneiventre*, were destroyed by natural enemies compared to the largely solitary *L. (D.) figueresi* (approx. 20% parasitism). This inter-specific comparison suggests social benefits due to mutualism (e.g., Lin and Michener, 1972), but data are not comparable since the species are not from the same locality at the same time. Additionally, the higher mortality in *L. (D.) figueresi* may be associated with the relatively longer development rate and the correspondingly longer exposure of larvae to mortality factors.

Temporal patterns of the life-cycle of *L. (D.) figueresi* are unusual for solitary bees (e.g. Linsley, 1958), and probably are not related to seasonal patterns of resource availability. Adult solitary females behave in ways similar to spring gynes of temperate eusocial halictine species (Michener, 1990) or gynes of some seasonally active neotropical eusocial species (Wille and Orozco, 1970). A temperate-zone gyne, for example, emerges from diapause in the spring, forages to collect pollen to provision several cells, and then stops foraging and waits inside her nest until brood emerge. The gyne then resumes egg-laying and dominates her female offspring, which become her workers (or later become replacement gynes). In like manner, female *L. (D.) figueresi* begin excavating nests at the start of the dry season, and provision some cells; then they cease provisioning in the middle of the dry season at a time when other *L. (Dialictus)* and many other bees are actively provisioning nests. Female *L. (D.) figueresi* remain within their nest until they die. No marked or very worn adult females were found to co-occur with their newly emerged, unworn, adult progeny, unlike the solitary *L. (Evyllaesus) villosulus* (Plateaux-Que nu et al., 1989).

Bees in a few populations of "eusocial" halictines have solitary behavior at high altitudes in temperate regions (e.g. Sakagami and Munakata, 1972; G. C. Eickwort, pers. comm.), presumably because of a shorter favorable season for provisioning than at lower altitudes. High altitudes in the tropics, in contrast, are usually not more

seasonal than lower altitudes, being relatively cooler the year round. It is therefore unlikely that environmental conditions associated with altitude account for the differences in social organization between *L. (D.) figueresi* and *L. (D.) aeneiventre*.

The slow developmental rate of *L. (D.) figueresi* effectively precludes overlap of generations, but the underlying proximate mechanism is not known. The usual range of developmental rates for halictine bees is 20 to 35 days, similar to the rate for *L. (D.) aeneiventre* (see Weislo, 1991). These rates vary with temperature and other factors such as the photoperiod (Kamm, 1974). Temperatures near the *L. (D.) aeneiventre* localities (San Antonio de Coronado) tend to be either slightly cooler or similar to temperatures at *L. (D.) figueresi* localities (San Antonio de Escazú), so it is unlikely that low temperatures explain the slow development of the latter, and there are no photoperiod differences. *L. (D.) figueresi* females use pollen from at least several plant species, although a major source of pollen is *Melampodium*, which is locally abundant. No other halictids have been recorded from this plant, and it is possible, but unlikely, that nutritional considerations account for the slow developmental rate. Another bee, *Pseudopanurgus aethiops* (Andrenidae), has been collected on *Melampodium* (Krombein et al., 1979), but its developmental rate is unknown (Rozen, 1967).

### Acknowledgements

WTW received an enormous amount of help from William Eberhard, Mary Jane West-Eberhard, and their family; likewise, Marla Spivak and Bryan Alvarez Spivak helped in many ways. They also participated in helpful discussions (with WTW), as did J. Altmann, W. Bell, G. Eickwort, R. Jander, R. Minckley, L. Packer, J. Wenzel, and especially C. Michener. For their critiques of the manuscript we thank B. Alexander, W. Bell, R. Jander, C. Michener, M. J. West-Eberhard, and two anonymous reviewers.

Financial support for WTW was generously provided by the P. L. Stouse Memorial Scholarship Fund, Department of Geography, University of Kansas (1985 and 1988); a Sigma Xi Grant-in-aid of Graduate Research; the Theodore Roosevelt Fund of the American Museum of Natural History; a Short-term Fellowship from the Smithsonian Tropical Research Institute; U.S.A. National Science Foundation grant BNS 82-00652 (C. D. Michener, P. I.); a NSF Doctoral Dissertation Improvement grant (BNS 87-01046); the University of Kansas Graduate College Travel Fund; a University of Kansas Summer Honors Fellowship; a University of Kansas Dissertation Fellowship that was supplemented by the H. B. Hungerford Fund, Department of Entomology, University of Kansas; and final preparations of the manuscript were made while supported by the Center for Insect Science, University of Arizona. This is contribution 3050 from the Department of Entomology, University of Kansas.

### References

- Anonymous, 1965. *Anuario meteorologico, año 1965*. Instituto Meteorologico Nacional, Ministerio de Agricultura y Ganaderia, San José, Costa Rica.
- Anonymous, 1982. *Anuario meteorologico, año 1982*. Instituto Meteorologico Nacional, Ministerio de Agricultura y Ganaderia, San José, Costa Rica.
- Clark, P. J. and F. C. Evans, 1954. Distance to nearest neighbor as measure of spatial relationships in populations. *Ecology* 35:445-453.

- Coen E., 1982. Climate. In: *Costa Rican Natural History* (D. Janzen, Ed.). University of Chicago Press, Chicago, pp. 35–45.
- Conover, W. J., 1971. *Practical Nonparametric Statistics*. John Wiley & Sons, Inc., New York.
- Eickwort, G. C., 1986. First steps into eusociality: the sweat bee *Dialictus lineatulus*. *Fla. Entomol.* 69:742–754.
- Eickwort, G. C. and P. F. Kukuk, 1990. The relationship between nest architecture and sociality in halictine bees. In: *Social Insects and the Environment* (Proc. 11th Internatl. Congr. IUSI, Bangalore) (G. K. Veeresh, B. Mallik and C. A. Viraktamath, Eds.). Oxford & IBH Publ. Co., New Delhi, pp. 664–665.
- Hicks, C. H., 1931. Notes on certain bees, with a consideration of the use of the abdomen in nest construction. *Can Entomol.* 63:173–178.
- Kamm, D. R., 1974. Effects of temperature, day length, and number of adults on the sizes of cells and offspring in a primitively eusocial bee (Hymenoptera: Halictidae). *J. Kansas Entomol. Soc.* 47:8–18.
- Krombein, K. V., P. D. Hurd, Jr., D. R. Smith and B. D. Burks, 1979. *Catalog of Hymenoptera in America North of Mexico*. Smithsonian Institution Press, Washington D.C. 2735 pp.
- Lin, N. and C. D. Michener, 1972. Evolution of sociality in insects. *Quart. Rev. Biol.* 47:131–159.
- Linsley, E. G., 1958. The ecology of solitary bees. *Hilgardia* 27:543–599.
- Michener, C. D., 1964. Reproductive efficiency in relation to colony size in hymenopterous insects. *Ins. Soc.* 11:317–342.
- Michener, C. D., 1974. *The Social Behavior of the Bees*. Harvard University Press, Cambridge, Mass. 404 pp.
- Michener, C. D., 1990. Reproduction and caste in social halictine bees. In: *Social Insects: An Evolutionary Approach* (W. Engels, Ed.). Springer-Verlag, Berlin, Heidelberg, New York, pp. 77–121.
- Michener, C. D., E. A. Cross, and H. V. Daly et al., 1958. Additional techniques for studying the behavior of wild bees. *Ins. Soc.* 2:237–246.
- Michener, C. D. and R. B. Lange, 1958. Observations on the behavior of Brazilian halictid bees. V. *Chloralictus*. *Ins. Soc.* 5:379–407.
- Michener, C. D. and C. A. C. Seabra, 1959. Observations on the behavior of Brazilian halictid bees, VI. Tropical species. *J. Kansas Entomol. Soc.* 32:19–28.
- Michener, C. D. and A. Wille, 1961. The bionomics of a primitively social bee, *Lasioglossum inconspicuum*. *Univ. Kansas Sci. Bull.* 42:1123–1202.
- Moure, J. S., CMF and P. D. Hurd, Jr., 1987. *An Annotated Catalog of the Halictid Bees of the Western Hemisphere (Hymenoptera: Halictidae)*. Smithsonian Institution Press, Washington D.C. 405 pp.
- Packer, L., 1990. Solitary and eusocial nests in a population of *Auglochlorella striata* (Provancher) (Hymenoptera: Halictidae) at the northern edge of its range. *Behav. Ecol. Sociobiol.* 27:339–344.
- Packer, L., 1991. The evolution of social behavior and nest architecture in sweat bees of the subgenus *Evylaeus* (Hymenoptera: Halictidae): a phylogenetic approach. *Behav. Ecol. Sociobiol.* 29:153–160.
- Plateaux-Quénu, C., L. Plateaux and L. Packer, 1989. Biological notes in *Evylaeus villosulus* (K.) (Hymenoptera: Halictidae), a bivoltine, largely solitary halictine bees. *Ins. Soc.* 36:245–263.
- Rozen, J. G., Jr., 1967. Review of the biology of panurgine bees, with observations on North American forms (Hymenoptera, Andrenidae). *Amer. Mus. Nov.* 2297:1–44.
- Sakagami, S. F. and C. D. Michener, 1962. *The Nest Architecture of the Sweat Bees*. University of Kansas Press, Lawrence. 135 pp.
- Sakagami, S. F. and J. S. Moure CMF, 1967. Additional observations on the nesting habits of some Brazilian halictine bees. *Mushi* 40:119–138.
- Sakagami, S. F. and M. Munakata, 1972. Distribution and bionomics of a transpalearctic eusocial halictine bee, *Lasioglossum (Evylaeus) calceatum*, in northern Japan, with reference to its solitary life at high altitude. *J. Fac. Sci., Hokkaido Univ., Zool.* 18:411–439.
- Simberloff, D., 1979. Nearest neighbor assessments of spatial configurations of circles rather than points. *Ecology* 60:679–685.
- Sinclair, D. F., 1985. On tests of spatial randomness using mean nearest neighbor distances. *Ecology* 66:1084–1085.

- Sokal, R. R. and F. J. Rohlf, 1981. *Biometry* (2nd ed.). W. H. Freeman & Co., New York, 859 pp.
- Tepedino, V. J., L. L. McDonald and R. Rothwell, 1979. Defense against parasitization in mud-nesting Hymenoptera: can empty cells increase net reproductive output? *Behav. Ecol. Sociobiol.* 6:99-104.
- Wcislo, W. T., 1990a. A new species of *Lasioglossum* from Costa Rica. *J. Kansas Entomol. Soc.* 63:450-453.
- Wcislo, W. T., 1990b. Parasitic and courtship behavior of *Phalacrotophora halictorum* (Diptera: Phoridae) at a nesting site of *Lasioglossum figueresi* (Hymenoptera: Halictidae). *Rev. Biol. Trop.* 38:205-209.
- Wcislo, W. T., 1991. *Natural History, Learning, and Social Behavior in Solitary Sweat Bees (Hymenoptera: Halictidae)*. Ph. D. Dissertation, University of Kansas, Lawrence, 204 pp.
- Wcislo, W. T., (in press a). Nest localization and recognition by the solitary bee, *Lasioglossum (Dialictus) figueresi* Wcislo (Hymenoptera: Halictidae), in relation to sociality. *Ethology*.
- Wcislo, W. T., (1992). Attraction and learning in the mating biology of solitary sweat bees, *Lasioglossum (Dialictus) figueresi* Wcislo and *Nomia triangulifera* Vachal (Hymenoptera: Halictidae). *Behav. Ecol. Sociobiol.* 31:139-148.
- Wenzel, J. W. and J. Pickering, 1991. Cooperative foraging, productivity, and the central limit theorem. *Proc. Natl. Acad. Sci. (USA)* 88:36-38.
- Wille, A. and E. Orozco, 1970. The life cycle and behavior of the social bee *Lasioglossum (Dialictus) umbripennis* (Hymenoptera: Halictidae). *Rev. Biol. Trop.* 17:199-245.
- Yanega, D., 1988. Social plasticity and early-diapausing females in a primitively social bee. *Proc. Natl. Acad. Sci., USA* 85:4374-4377.

Received 20 August 1991;  
revised 1 June 1992;  
accepted 7 July 1992.