Seasonal cycles, nests, and social behavior of some Colombian halictine bees (Hymenoptera; Apoidea)[1]

by

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Abstract: This paper contains descriptions of nests and information on seasonal cycles and social behavior of four halictine bees, *Habralictus bimaculatus, Caenohalictus eberhardorum, Lasioglossum (Dialictus) seabrai,* and *L. (D.) breedi.* Data are also included on two parasitic halictine bees, both of the genus *Microsphecodes.* The *Habralictus* and *Caenohalictus* nest in aggregations; individual nests are occupied by one to several bees. There are no castes and within a nest containing two or more bees the relationships are communal or possibly quasisocial. The two species of *Lasioglossum (Dialictus)* nest in diffuse and often small aggregations. The colonies have mean populations of little over two bees, but there are weakly differentiated queens and workers, especially in *L. seabrai.* Activities were similar in both wet and dry seasons, so far as known.

The purpose of this paper is to provide new data on the biology of halictid bees, particularly those which are intermediates between solitary and eusocial or which are primitively eusocial. The present treatment deals with four social species and two parasitic species, the taxonomy of which is dealt with in a companion paper (Michener, 1979). Studies of such species provide insights into the origin and evolution of social behavior among bees. Our knowledge of primitively eusocial halictids and of various intermediates between solitary and eusocial species is summarized by Michener (1974); subsequent papers are by Breed (1975), Michener and Bennett (1977), and Litte (1977). A series of recent papers on the behavior of *Lasioglossum zephyrum* in laboratory colonies is reviewed by Michener (1977a). The recent finding of a hitherto unknown type of social organization in tropical populations of *Halictus ligatus* (Michener and Bennett, 1977) illustrates the

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potential for interesting discoveries. The present paper is a result of studies of halictid bees in an area where no prior work on their behavior had been conducted, the Colombian Andes. All species treated below are in the tribe Halictini; the only important information obtained on the same trips for the tribe Augochlorini has already been published (Michener, 1977b).

MATERIAL AND METHODS

The nest-making bees as well as the associated parasitic bees are all small species discussed or described by Michener (1979). The species involved are *Habralictus bimaculatus* and its parasite *Microsphecodes truncaticaudus, Caenohalictus eberhardorum, Lasioglossum (Dialictus) breedi* and its parasite *Microsphecodes trichommus,* and *Lasioglossum seabrai.* Data were obtained by observations at nest entrances, excavations of nests, and subsequent measurements, dissections, and evaluations of wing and mandibular wear of female bees taken from nests, as well as of samples of females performing specific activities (e. g., foragers returning to nests with pollen). Specimens were preserved in Kahle's (Dietrich's) solution and dissected later. All important techniques were among those described by Michener *et al.* (1955).

In addition to measurements of ovarian width and length of the longest oocyte, ovaries were classified as follows: A, conspicuously enlarged, width over 0.25 mm, longest oocyte well formed, over 0.75 mm in length; B, moderately enlarged, width 0.15 to 0.35 mm, longest oocyte less than 0.75 mm in length, usually not shaped like an egg ready to be laid; C, slender or only locally enlarged, occasionally reduced in size below that found in callow adults, width 0.06 to 0.16 mm; D, slender, uniformly tapering, entirely without enlargements, as in freshly emerged or callow adults, width 0.10 to 0.15 mm. The distinction between C and D was sometimes difficult and in such cases was made on the basis of wear. All individuals classified as D were entirely unworn while those classified as C showed some wear.

Spermathecal contents are indicated by the following symbols: + = with sperm cells, o = empty, — = unknown because the spermatheca was lost in dissection.

Mandibular wear was coded on a scale like that for *Lasioglossum imitatum* as illustrated by Michener and Wille (1961); 1 was unworn and the maximal number for the species represents maximal wear observed.

Wing wear (number of nicks in the margins) was recorded for all individuals but as usual in small bees, the wings are not much worn; although bees with nicked wings always had worn mandibles, many with well worn mandibles had unworn wings. Wing wear is erratic, presumably resulting from chance brushing against vegetation during flight. Mandibular wear alone is therefore used in this paper as an indication of past activity.

In summarizing attributes of individual bees, the ovarian condition, spermathecal contents, and mandibular wear are expressed in symbols such as A + 3, meaning ovaries of Class A (enlarged), mated, with mandibles worn to Class 3.

Field work by all the authors was carried out in September and October, 1976, continued through October by Bell and Breed, and resumed in January and February, 1977, by Breed and Michener, with monitoring of populations by Lucy Gonzales de Cuadros in March, May, and June, 1977. Limited earlier observations or collections of some of the species were by Michener in January, 1972, and by W. G. Eberhard and M. J. West Eberhard in April, 1972. Dissections and measurements were made by Breed; preparation of the manuscript and illustrations was by Michener.

Nesting sites: All nesting sites studied (designates A to F) are in the western range of the Andes, west of the city of Cali, Provincia del Valle. Sites A to E are not far from the Cali to Buenaventura highway which crosses the summit of the range at a point 18 km west of Cali. Site A is along a side road north from that point, about 2 km from the highway. Above the site is montane forest, almost cloud forest, while across the road below the site most of the area has been cleared except for scattered trees, and is used primarily for pasture. The altitude is about 2000 m.

Above the town of Salidito on the east side of the range, a road leads generally south from the highway to the town or district of San Antonio, and on to a television transmission tower on the summit of the range. Sites B and C are banks along this road, B about 200 m from the highway, C about 2 km from the highway and at the edge of San Antonio. Both are near edges of montane forest patches, conspicuously drier than the forest at Site A, but most of the surrounding area is pasture. The altitude is about 1800 m. The site at which Michener studied some of the same species in 1972 is along the same side road, farther toward the television tower, and is termed Site D.

On the west side of the range a side road descends from the highway southward to the town of El Carmen. Site E is along this road, about 2 km from the highway, at the edge of a forest patch in an otherwise deforested pasture area. The altitude is about 1900 m.

Site F is above Pichinde, 1630 to about 1900 m altitude, again at the edges of areas of montane forest which occupy the steep slopes, with cultivated and pasture land elsewhere.

Climate: Among the most equable climates in the world are those of middle altitudes in the tropics. To us the weather always felt warm when the sun was shining, cool when overcast. Data are not available for the immediate vicinity and altitude of our study sites; the weather is obviously quite different from that of the nearby city of Cali (altitude 1,000 m). Even at the height of the dry season, when grass fires are prevalent near Cali, pastures are largely green in the vicinity of our sites. Fog and low clouds are frequent at the altitude of our sites, sometimes keeping the bees in the nests for days at a time, especially in the wet season, but during most days the clouds break and allow a few minutes to an hour or so of foraging before covering the area again.

The seasons, while variable from year to year, are roughly as follows (M. J. West Eberhard, *in litt.):* major dry season, mid July to mid September; less regular minor dry season, December and January. The rest of the year is wet, wettest from March to May and October and November. The major dry season in 1976 was intense and protracted, continuing into early October, and January and February were also rather dry. Thus the studies reported here were begun in an unusually dry period (September, 1976), carried on into the following wet season (October, 1976), resumed in a moderately moist period (January and February, 1977), and carried on by netting specimens at the nest sites, thanks to L. Gonzales de Cuadros, through the wet season until June.

HABRALICTUS BIMACULATUS

Nest sites: Large numbers of nests were in a vertical, east-facing, roadside bank of soft but firm, decomposed rock at Site A. This was by far the most common bee inhabiting this bank. The bank was about 2 m high and 2.5 m long. In some areas, especially near the top of the bank, nest entrances were separated by only 2 to 4 cm while in other areas they were sparser. Site C was a vertical roadside bank inhabited primarily by *Caenohalictus eberhardorum*, but an area about 20 cm in diameter near the foot of the bank contained nests of *H. bimaculatus.* This bank also faced east and was composed of firm, fine soil derived from the bed rock and still showing some of the structure of the rock. Site D was similar in orientation; the area occupied by nests was not determined. At Site E a roadside bank facing northwest contained near its base a few nests of *H. bimaculatus,* and at Site F a similar bank facing north contained sparse nests of this species. All the banks were largely covered with liverworts and mosses and the nest entrances were therefore often hidden from view by these plants. Excavated soil, however, often revealed locations of nests. Removal of vegetation with a trowel or knife exposed the entrances, and in subsequent weeks the bees continued to use such visible entrances, apparently as freely as those hidden by mosses. No nests were found in situations where higher vegetation, such as grasses, was dense.

Seasonality: This species is probably active throughout the year. Females were recorded carrying pollen loads into nests in September, October, January, and February. No effort was made to record such behavior in other months, but females with enlarged ovaries, with eggs more or less ready to lay (Class A), were taken in these same months as well as in March, May, and June. New nests, as yet without cells or with only a roughed out cell, were found in September, January, and February. Males were taken flying about the nest sites in all these months except June, and also in April. We saw about the same amount of activity in September and October as in January and February, and the collections of L. Gonzales de Cuadros suggested similar activity in subsequent months.

Short term fluctuations in activity due to weather or foraging conditions doubtless occur and are suggested by the following census of 84 cells (from numerous nests) at Site A on February 6:

open, without young, 2
eggs, 20
small larvae, 2
medium sized larvae, 2
large larvae, 1
prepupae, 3
male pupae, 17
female pupae, 16
callow adult males, 13
callow adult females, 4
Microsphecodes pupae, 4.

The scarcity of larvae suggests a recent period of reduced activity, terminated by much recent egg laying.

Nests (Figs. 4 and 5): The main burrow is about 2 mm in diameter, more or less horizontal although somewhat winding, usually ending at a depth of 8 to 16 cm, although one at Site E extended to 20 cm and one at Site D to a depth of 26 cm. Usually the burrow extends deep into the bank but sometimes it curves and may be largely parallel to the surface of the bank. The burrow entrance is noticeably constricted. Lateral burrows extend horizontally or downward from the main burrow, each ending in a single cell. These laterals are 4 to 20 mm long ($x = 11.1$ mm, $N = 12$), 2 mm in diameter, scattered irregularly along the median part of the main burrow, which commonly extends considerably deeper than any laterals. Although laterals do not arise closer than about 3 cm from the entrance of the main burrow, curvature of the latter results in some cells as close as 1 cm from the surface of the bank; others are as deep as 12 cm into the bank. When a cell is completed, the lateral is filled with soil so that a given nest has only from one to three open laterals leading to cells being constructed or provisioned. The density of the intertwining nests, the irregularity of the curves of the main burrows, and variations in length and direction of the usually earth-filled laterals, combine to make careful excavation of nests of this species frustrating and conclusions as to numbers of cells and of bees per nest somewhat dubious.

The cells are 6 to 7 mm long, 2.5 to nearly 3 mm wide, shaped as usual in Halictini, lined with the usual thin, smooth, waxlike layer. Cells slope slightly downward from their entrances, the main axis of a cell being 15 or 20^{o} from horizontal. The pollen ball is somewhat flattened, the upper surface where the egg is placed being less convex than the other surfaces. The horizontal diameters of a pollen ball are about 2.25 mm, the vertical diameter about 1.75 mm. The larval feces are placed in the position usual for halictines, on the distal and upper surface of the cell.

The maximum number of cells found in a single nest was eight. There is a tendency for all the cells in a nest to contain immatures in about the same stage. The cell contents of the only nests sufficiently isolated that we probably found most or all of their cells and did not get them confused with those of other nests are listed below:

1. Sept. 17: 5 medium to large larvae
2. Sept. 17: 1 medium, 1 large larva; 1 pupa; one abandoned cell
3. Sept. 17: 4 pupae
4. Jan. 9: 5 eggs
5. Jan. 9: 3 pupae
6. Jan. 9: 3 small to large larvae
7. Feb. 5: 2 with pollen; 2 eggs; 2 small larvae; 2 medium larvae.

Old cells, from which bees have emerged, are earth filled, suggesting that the young adult digging its way out through the lateral burrow pushes soil back into the cell from which it has emerged.

Longevity and sociality of females: The fact that young in a given nest tend to be of the same age indicates that a female works over a brief period to produce a brood, and then (a) dies, (b) leaves to make other nests elsewhere, or (c) becomes inactive and resumes cell construction and reproduction in the same nest after emergence of the first brood. The last possibility is unlikely, for if it were so, one should find a class of ovarially inactive females waiting to resume activity. This is not so; virtually all of the 39 mature females dissected (October, February, March, May, and June) had enlarged ovaries. If they leave to nest elsewhere over a long life, one would expect to find them as badly worn bees. In fact, almost all the bees had unworn wings and mandibular wear of class 2 or 3. We therefore believe that the females are relatively short-lived and provision several cells at about the same time (to the extent permitted by the weather) and then die. The rather small number of cells found per nest suggests that a bee may make a second or third nest. A nest containing older larvae and pupae did not always contain any adult, and was often not recognizably open at the surface; presumably the mother or mothers had died or abandoned it.

Individual nests were sometimes inhabited by single bees, sometimes by several. In 15 nests whose adult female inhabitants could be counted, the number ranged from one to six with a mean of 2.3. Three new nests containing no cells, or only a roughed-out cell, were each inhabited by two bees, suggesting that a bee that has started a burrow may soon be joined by another. In other cases old cells near a nest burrow occupied by several bees suggested that inhabitants of a nest might be young that emerged into it.

There is no evidence of division of labor among the females in a nest. There are no guards at nest entrances. There is no evidence of a worker caste. Of 39 bees taken from nests inhabited by more than one bee, and subsequently dissected, 33 had ovaries of Class A. All of these whose spermathecae were examined had mated. The remaining 6 bees with more slender ovaries included one parasitized by a strepsipteran, one with abnormal minute ovaries (smaller than in a newly emerged adult), two callows (wings wrinkled and soft), and two that were not callows but were unworn, probably young, one of them with an empty spermatheca. A sample of eight pollen collectors caught as they returned to their nests were similar to the ordinary nest bees, all with enlarged (Class A) ovaries, sperm cells in the spermatheca, unworn wings, and mandibular wear of Class 1 to 3.

From the above paragraph it is apparent that normal females mate, forage, and lay eggs. Probably they all make cells as well. Nonetheless the colony does not always appear to be of the typical communal type (Michener, 1974) in which each female makes and provisions her own cells, for we sometimes found more foragers carrying pollen into a nest than there were cells being provisioned or ready to provision. Presumably some cells are provisioned by two or more bees. To document this, we plugged eight nest entrances at Site A on February 8 (11:00 a.m) and captured returning bees, all of them carrying pollen loads. After an hour, when such foragers were no longer seen, presumably all having returned, we excavated the nests, captured any additional bees therein, and counted the number and condition of open cells. The results are tabulated below:

1. 1 pollen collector, 1 empty cell
2. 1 pollen collector, 1 empty cell
3. 1 pollen collector, 1 cell with little pollen
4. 1 pollen collector, 1 empty cell, 1 cell with little pollen
5. 3 pollen collectors, 2 empty cells
6. 3 pollen collectors, 1 empty cell, 1 cell with little pollen
7. 3 pollen collectors, 1 other bee, 1 cell with little pollen
8. 4 pollen collectors, 2 other bees, 1 emptycell, 4 cells with little pollen.

In all, there were 20 adult females (17 known to be foragers) associated with 16 cells that might have been receiving pollen. Excluding nests 1 to 4 which contained only one adult bee each, there were 16 adults associated with 10 cells that might have received pollen. There is nothing to suggest that the "other bees" in nests 7 and 8 are anything but foragers that happened to be in their nests when the entrances were plugged.

Nests 5 to 7 suggest that cooperation in cell provisioning occurs, since the number of foragers exceeded the number of open cells. Such colonies would be quasisocial (Michener, 1974). The colony in nest 8 could be communal. The bees in nests 1 to 4 were solitary. Quasisociality is a rare condition and should be verified by work at sites where the nests are well isolated, so that nearby nests do not confuse one's findings.

Male behavior: Whenever the sun was shining, and sometimes when it was not, males were to be seen flying close over the surface of the bank where the nests were located or over nearby vegetation. Males sometimes pounced of females but mating was not observed. Nonetheless, it seems probable that matingregularly occurs around the nesting site, not on the flowers or elsewhere.

CAENOHALICTUS EBERHARDORUM

Nest sites: Thousands of nests at Site C occupied part of a vertical roadside bank that faced east. Although the bank was about 100 m long, these bees occupied only a portion about 8 m long and 1 m high. At Site D males flying about the bank indicated the presence of nests, but none were excavated. At Site E a portion (about 2 x 2.5 m) of a large roadside bank facing northwest was occupied by many nests of this species, and at Site F several locations in banks facing north contained a few, scattered nests. Some of the banks were covered with liverworts and mosses, others (at E and F) were largely bare. The nest entrances were larger and more conspicuous than those of *Habralictus bimaculatus,* although especially on mossy banks the loose soil below nest entrances is the only easily seen indication of the locations of nests.

Seasonality: As in *Habralictus bimaculatus,* this species is probably active throughout the year. The first paragraph under this subheading in the account of *H. bimaculatus* applies equally to this *Caenohalictus,* although new nests as yet without immature stages were recognized only in September and February. The aggregations are denser than those of *Habralictus,* and perhaps for this reason males and females were taken in all months of the study, September, October, January, February, March, April, May, and June.

Short term fluctuations in activity due to weather and availability of food are suggested, as for *H. bimaculatus.* Censuses of cell contents from various nests show such fluctuations, as indicated by the numbers of cells with young in various stages from Sites C and E (first and second columns of numbers below) taken on February 2 and 5, 1977:

open, empty cells	1	1
eggs	1	4
small larvae		1
medium larvae		4
large larvae	1	2
prepupae		2
male pupae	26	8
female pupae	25	11
callow adult males	10	3
callow adult females	5	2

At Site C foraging and production of young had virtually stopped as shown by the small numbers of eggs and larvae, shown in the first column of figures above, while at Site E they continued, as shown by the second column.

Nests (Figs. 1 and 2): The nests are similar in many ways to those of *Habralictus bimaculatus* but because of their density, irregularity, and the long laterals which are earthfilled after completion of the cell to which each leads, it was impossible to make complete excavations and diagrams for many nests. The main burrow is about 2.5 mm in diameter, 7 to 20 cm deep ($\bar{x} = 14.9$ cm, $N = 12$), irregular, often winding, more or less horizontal, lined with a thin layer of fine soil. The burrow entrance is gradually constricted in the 10 to 15 mm nearest the surface of the bank, to 2 mm or slightly less in diameter at the surface. (In most halictines the constriction is limited to the immediate vicinity of the entrance.) Lateral burrows, each leading to a single cell, are roughly horizontal, not lined with fine soil, only 2 mm in diameter, noticeably smaller than main burrows, but the apparent distal part of the main burrow, possibly to be called an inward-directed lateral, may also be 2 mm in diameter. Lengths of lateral burrows ranged from 4 to 42 mm (all but one 15 mm or more. $\bar{x} = 23.6$ mm, $N = 21$). Laterals arise at irregular intervals along the main burrow, not in the 2 to 3 cm nearest the entrance, and mostly are directed somewhat inward away from the surface of the bank. Cells were found from 3 to 20 cm from the surface of the bank. After a cell is completed and an egg laid in it, the lateral leading to it is completely filled with earth. Active nests have only one to three open laterals leading to cells being constructed or provisioned.

The cells are 6-7 mm long, 3 mm in diameter, similar in structure and slope of their axes to those of *Habralictus bimaculatus*. The provisions are also similar to these, as are larval feces and old cells.

The maximum number of cells associated with a single nest was eight, but the accuracy of this figure is even more subject to doubt than is that for *Habralictus bimaculatus* because of the intertwining burrows and long laterals. Again, there is a tendency for the young in any one nest to be of about the same age, as shown by the following lists of cell contents of the only nests that were more or less completely excavated:

1. Sept. 22: 1 small larva; 3 laterals without cells
2. Sept. 22: 4 small larvae
3. Sept. 24: 4 pupae
4. Sept. 24: 4 pupae
5. Sept. 24: 7 pupae, 1 callow adult
6. Sept. 24: 2 pupae, 1 callow adult

7. Feb. 3:	1 larva, 2 pollen balls
8. Feb. 5:	2 pollen balls
9. Feb. 15:	1 empty cell, 1 cell with pollen.

Longevity and Sociality of Females: The evidence and conclusions as to these topics are about the same as for *Habralictus bimaculatus*. All the 34 non-callow females in all nest populations taken had enlarged (Class A) ovaries, the longest oocyte of each female being 0.75 mm long or longer, and all were mated with the possible exception of a few whose spermathecae were lost. The only non-callows with slender ovaries that we found were a few unworn, sometimes unmated individuals among those flying about the bank surface. Presumably they were young adults seeking nest sites.

The evidence about social organization is also similar to that for *H. bimaculatus*. The nest aggregations tend to be denser than in that species and at Sites C and E occupied only small parts of large banks. Thus the social nature of the aggregations is very probable. In 18 nests into which pollen-carrying bees entered, populations of adults ranged from 1 to 5 with a mean of 1.8. New nests, as yet without immature stages, sometimes contained two adult females. Of 22 bees from nests inhabited by more than one female, and subsequently dissected, all had enlarged (Class A) ovaries with the largest oocyte 0.94 mm long or longer and all had mated with the possible exceptions of a few whose spermathecae were lost in the dissection process. Fourteen pollen collectors were similar except that one lacked sperm cells in the spermatheca. Wing and mandibular wear was as in the *Habralictus*.

Only two nests that we excavated had more bees in the nests than cells open. Thus the evidence for communal colonies (sense of Michener, 1974) is no stronger than for *H. bimaculatus* and we suspect that the apparently quasisocial colonies of both species may result from our failure to find certain cells during the excavations. Ten nests out of 18 were apparently constructed by lone individuals.

Male behavior: Whenever the sun was out and sometimes when it was hidden by clouds, males flew about the nesting area at Site C in enormous numbers, such that if there was no wind the sound of their wings could be heard 2 m from the bank. At other sites males flew similarly but in lesser numbers. Most of the flight is within 5 cm of the bank surface, and the individuals continue in flight for long periods, alighting only occasionally and momentarily. On some occasions no mating was observed, although pouncing on females, including those carrying pollen, was common. On other occasions, probably when numerous young females were emerging, matings occurred frequently. Males often pounce on females as they leave nest entrances (there are no guards). Sometimes a male hits a female in the air and knocks her down. The male takes the usual position for mating, but often other males then pounce on the pair so that a mass of five or six may form, which then often tumbles down the bank, all the bees quickly flying off. Undisturbed matings are rather long for halictids, probably one or two minutes; we saw few and timed none that were undisturbed by other males from beginning to end.

To get information on the flight behavior of individual males, several were netted on September 24 in a small space (50 x 50 cm), marked with paint, and liberated at a distance of 5 m. In 10 minutes the marked bees were back in the area on the bank from which they had been netted, suggesting that they recognize particular areas and do not fly all over the bank.

Each marked bee flew in its limited range. One was in a small depression in the bank, 10 cm wide and 30 cm high. Others were in more or less circular areas about 30 cm in diameter. One was hard to observe because its range was under an overhang and largely in shadow. Only occasionally did a bee fly for a few centimeters outside its range. These ranges are not mutually exclusive territories. Other bees fly in the same areas although interactions among males were never apparent. Ranges of many bees broadly overlap but no two were seen to be identical. Four days after marking, marked bees were seen flying in the same ranges that they had occupied earlier. Unfortunately we do not know whether a given range is occupied for the life of a male or whether its range includes the nest entrance from which it emerged.

Each male's flight pattern on its range consisted of an irregular zigzag upward to the summit of the range. It then quickly dropped more or less straight down to the bottom of the range, and repeated the upward zigzag flight (Fig. 3).

LASIOGLOSSUM (DIALICTUS) SEABRAI

Nest sites: This species, easily distinguished in the field from other *Dialictus* by the dark-tipped wings, was found nesting at several sites. For comments on the identification of this species, see Michener (1979). In no case did the nests form dense aggregations; they were scattered, occasionally two or three only 5 to 10 cm apart, but mostly more widely spaced. At Site A two nests were found in the vertical bank among nests of *Habralictus bimaculatus*, eight were in the clay soil of the horizontal roadway one to four meters from the bank and mixed with nests of *L. breedi*. At Site B several nests were found in a roadside bank that faced eastward and sloped at an angle of about 45°. At Site C two nests were in the vertical bank among nests of *Caenohalictus eberhardorum*, while a few others were in the same bank outside of the *Caenohalictus* area and in sloping soil at the base of the bank. At Site E nests were mostly in flat ground but some were in the sloping sides of a ditch at the base of a bank. Most of the nests were in bare ground, a few in mossy banks, and some among small clumps of grass or weeds.

Seasonality: Foraging and cell provisioning, young callow adults in cells, and flights of males were all seen in September, October, January, and February. Males in considerable numbers were caught near the nest sites by L. Gonzales de Cuadros in March and she netted two unfertilized young females in May and June. New nests, i. e., burrows without cells or with only new cells containing pollen or eggs, were found in September, October, January, and February. Simple burrows, inhabited by a female with no cells, could represent bees in an inactive stage but in each month listed nests with no cells except newly provisioned ones were also found. We therefore interpret the simple burrows as probable new nests, a view supported by the presence of fresh dirt at the entrances (tumuli, or earth falling from the entrances of nests in banks). Because of the diversity of seasons in which these observations were made, it seems likely that similar activity goes on throughout the year. Failure to capture males in the cool, wet weather of May and June may reflect inactivity of males present, but there could be a life cycle that produces few males in that season.

Nests (Fig. 8): Nests fall within the range of the usual *Dialictus* style (Sakagami & Michener, 1962). The main burrow is somewhat irregular, not straight, roughly vertical when in flat ground and sloping at an angle of about 45° when in banks. The diameter of the burrow is 3 to 3.5 mm, constricted at the entrance. The entrance is plugged with soil in foggy, rainy or heavily cloudy weather but is soon opened when sun strikes the nesting site. Depths of nests with cells range from 11 to 19 cm ($\bar{x}$ = 13.3 cm; N = 12). The burrow is simple or in three cases out of 12, with a short branch, less than one cm long, near the bottom.

The cells are of the type usual for *Dialictus*, nearly horizontal and almost sessile. The closure is of rather loose soil about 2 mm thick. Cell depths ranged from 4 to 12 cm ($\bar{x}$ = 7.5 cm; N = 23). Most cells were scattered along the middle parts of burrows, the depths of the uppermost cell ranging from 4 to 10 cm. Sometimes three or four cells radiated from the burrow at about the same level. In three nests there was a cell very near the bottom of the burrow.

The number of occupied cells and fresh cells being provisioned in a nest varied from zero to four. There were often a few additional old, earth-filled cells, from which bees had emerged. The mean number of cells (excluding old, earth-filled ones) in the nests examined was 1.5 but among the 12 nests with at least one cell, the mean number was 1.8. This low number indicates protracted reproductive activity, perhaps associated with the long, probably year-long, season of activity. Small bursts of activity occur, however, for in six nests there were two cells in approximately the same stage (e. g., 2 cells with eggs, or 1 egg and 1 young larva) and in one nest there were three such cells. Otherwise substantial developmental gaps separated the young in different cells of a nest (e. g., 1 egg, 1 large larva). With one exception nests with two or three cells in about the same stage contained more than one adult, and that exception may not have been real for the nest was dug by us when the sun was shining and one or more bees may have been foraging, although we saw no such bee return to the site.

Sociality of females: The number of adult bees in nests examined ranged from one to three. In 12 nests that contained cells, the mean number of adults (excluding callows) was 2.1 In six nests listed below, whose bees were all dissected, if one excludes one callow and an unworn, unfertilized bee with threadlike ovaries that was probably young, five colonies contained only two bees and one three. The mean number of all adults in the seven nests containing two or more adults was 2.3. Thus the usual number of mature, working adults in a colony is only two. In all nests, including those without or with only abandoned earth-filled cells, the mean number of adults was 1.5. Clearly the nest populations of this species are extremely small.

All 8 nests without cells and one with only old, earth-filled cells contained only one adult. Dissections showed such bees to be mostly fertilized, with ovaries ranging from classes A to C. Seemingly, lone bees start nests, undergo ovarian enlargement, make and provision cells, and lay as solitary bees would. The presence of two adults each in two nests that contained no cells old enough to have produced adult offspring and no remnants of old, earth-filled cells suggests, however, that nest makers are sometimes joined by other individuals to form temporarily semisocial colonies.

The other colonies, in nests containing older immature stages, nearby old cells, and such evidence of long activity, are highly variable in attributes of colony members, as indicated by the following tabulation of ovarian development, mating, and cell contents (attributes of each bee are indicated between commas, using the system described under Material and Methods):

1. Oct. 27: B+3, Co2, Do1 (callow); 2 cells with pollen
2. Jan. 31: B+1, Bo2, B-1; 2 cells with eggs
3. Jan 31: Bo2, Co5; 1 new cell, 1 with pollen ball
4. Feb. 1: A+5, Bo5; 3 cells with eggs, 1 prepupa
5. Feb. 1: A+5, Bo1; 1 large larva, 1 prepupa
6. Feb. 6: A+3, Bo1; Do1.

Familial relations among the adults cannot be established from our meager data. In colonies like those in Nests 2 and 4, all are probably of about the same age and our impression is that these are not matrifilial colonies. The same could be true for Nests 1, 5, and 6, but the first bee listed for each of those colonies could be the mother of the others, i. e., the queen, being fertilized while the others are not, as well as more worn and with larger ovaries. In view of the prevalence of matrifilial colonies in *Dialictus,* it is probable that eusocial as well as semisocial and mixed colonies exist in this species.

The data suggest that the principal egg layer (queen) is on the average larger than other bees in her nest. The bees in Nest 2 above were all about the same size. For the other nests, however, the first bee listed was the largest in each nest except Nest 6, in which the first and second were of equal head width. (The wings of the first bee in Nest 6 were too worn to measure, so that a comparison of wing lengths is impossible.) The bee with the largest ovaries is also commonly fertilized while others are not.

These observations suggest castes similar to those found in most other species of *Dialictus,* in spite of the very small size of the colonies of *L. seabrai.* To further explore the possibility of castes, we assembled data on head width, wing length, mandibular wear, ovarian class (A to C, D being immature and irrelevant for this purpose in this species), and mating or lack of it (as determined by presence or absence of a ball of sperm cells in the spermatheca), for nest populations together with samples of bees taken on the wing in the nesting areas. No significant relationship was found between wing wear and ovarian development, perhaps because wing wear is a chancy and therefore poor indication of activity in these small bees whose wings often do not become worn at all. Mandibular wear, although ranging from 1-5 in bees of each ovarian class, was on the average significantly less for bees with Class B ovaries than for those with ovaries of Classes A and C. [Ovarian Class A, mean mandibular wear ($\bar{x}$) = 3.40, SD = 1.454, N = 15; B, $\bar{x}$ = 1.88, SD = 1.310, N = 16; C, $\bar{x}$ = 3.29, SD = 1.383, N = 14.] The difference in wear for Class A and B individuals is significant at $p < .05$, while for B vs. C the wear differs at $p < .01$. Perhaps these data mean that some Class B individuals develop into Class A queens, while others may regress to Class C workers, so that on the average Class B individuals are younger and less worn than bees of the other two ovarian classes.

Spermathecal content considered in connection with ovarian development clearly demonstrates the existence of a non-mating worker class. Of 16 individuals in ovarian Class C whose spermatheca were examined, only one had mated. By comparison, all 13 individuals in ovarian Class A had mated, as had 6 out of 15 individuals in Class B.

As to size, individuals of ovarian Class A were significantly ($p < .05$) larger both in head width and wing length than were those of Classes B + C. Classes B and C did not differ significantly from one another in either measure of size. A was significantly larger than B in head width, and than C in wing length. These results are based on 14 to 16 individuals of each ovarian class; significance of differences in means was determined by analysis of variance. Data are as follows:

Ovarian Class A, head width: $\bar{x}$ = 1.38 mm, SD = .049, N = 15
wing length: $\bar{x}$ = 4.06 mm, SD = .163, N = 14
Ovarian Class B, head width: $\bar{x}$ = 1.34 mm, SD = .062, N = 16
wing length: $\bar{x}$ = 3.97 mm, SD = 1.25, N = 16
Ovarian Class C, head width: $\bar{x}$ = 1.34 mm, SD = .073, N = 14
wing length: $\bar{x}$ = 3.92 mm, SD = .182, N = 14

It is apparent that the size difference between workers and queens is slight.

Among 24 individuals carrying pollen loads taken as they approached their nests in February (Site A), 10 were in ovarian Class A, 4 in B, and 10 in C. Thus over half the foraging population had markedly enlarged ovaries. Some were probably lone individuals, not living in colonies. We do not know whether the one or two workers in a colony inhibit foraging by the queen.

Male behavior: Males were only rarely found flying about the nesting areas or about flowers. At Site A and particularly at Site E, males were seen in dancing or swarming flight about the tops of plants 0.5 to 3.0 m above the surface of the ground, 2 to 10 m from the nearest known nests. Such males alight occasionally on leaves, especially when a cloud obscures the sun, but spend much of the time in the air. This flight behavior was observed from 9:00 a.m. to 1:00 p.m. Females occasionally alight on the same leaves. Twice we saw a male pounce on such a female but mating did not take place. Nonetheless we believe that the usual mating place for this species is neither around the nests nor around flowers, but on foliage of herbaceous and bushy plants in the general vicinity of the nests.

LASIOGLOSSUM (DIALICTUS) BREEDI

Nest sites: This small black bee (hesitantly included in *Dialictus*; Michener, 1979) was found nesting abundantly at Site A. A very few nests were in the bank among those of *Habralictus bimaculatus* but the majority were in the flat, hard-packed soil of a roadway, intermixed with small numbers of nests of *L. seabrai*. At Site F several nests were found in less compacted flat ground beside a road, and a few others in a steep but not vertical roadside bank. At both sites the flat ground inhabited by this species was bare or nearly so. At both sites, also, the nests seemed aggregated. Thus at Site A, although we walked repeatedly along some 3 km of road seeking nests, we found them only in a stretch about 15 m long. There were sections of the road that had too much gravel or were otherwise unsuitable, but numerous apparently suitable areas lacked nests as is often the case in related bees (Batra, 1966).

Seasonality: We found the bees active in September (end of a very dry season) and except as flight was inhibited by fog and rain, in late October (beginning of wet season), as well as in January and February (a relatively dry period but much wetter than in the previous September). In September, October, January, and February we found nests being initiated, newly provisioned cells, as well as all immature stages. The number of immature stages per nest was less in September and October than in January and February, but under a variety of weather conditions, activity, nest contents, and the like seemed not greatly changed and we suspect the species is active throughout the year. However, for the other month, when we were not in Colombia, we have only a single, apparently young, unworn and unfertilized female taken in June. The males do not have flight patterns that make them easily captured, like those of the other species treated in this paper, and the females fly close to the soil surface and are inconspicuous. The mere lack of information for other months, therefore, may not indicate inactivity by the species during those months.

Nests (Figs. 6 and 7): The nests are of the general type of those of other *Dialictus*. The main burrow, in the one nest excavated in a vertical bank, sloped downward only about 15° from the horizontal. The great majority of the nests, those in flat ground, have more or less vertical burrows although some slope; one was at about 40° from the vertical. The diameter of the burrow is 2.5 to 3.5 mm, constricted at the entrance to a diameter of 1.5 to nearly 2 mm. The entrance is plugged with soil, sometimes to a depth of several millimeters, in foggy, rainy, or heavily clouded weather but is often opened soon after the sun strikes the site. Symmetrical tumuli up to 15 cm in diameter accumulate around entrances of new burrows in flat ground, but in a wet climate small tumuli such as these are ephemeral. Depths of nests with cells ranged from 3.5 to 10 cm ($\bar{x}$ = 5.28 cm, SD = 1.524, N = 53). The burrow is simple except that two of 53 nests were branched like an inverted Y near the middle.

The cells are similar to those of most *Dialictus* (Sakagami & Michener, 1962), nearly horizontal but with main axes sloping slightly downward toward the distal ends. Cells are about 6 mm long (measurements of the part with waxlike lining), 3 to 3.5 mm in diameter, each separated from the main burrow by a short lateral 2 mm in diameter and 4 to 7 mm long. Thus the distal ends of cells are 10 to 13 mm from the main burrow. The laterals are completely filled with soil to close the cells after oviposition. Cell depths range from 1 to 5 cm ($\bar{x}$ = 3.4 cm, N = 40). Most of them join the middle or upper parts of main burrows, the uppermost cell ranging from 1 to 4 cm in depth ($\bar{x}$ = 2.2 cm, N = 24). Often three or four cells radiate from the main burrow at about the same depth.

The number of occupied cells and cells being provisioned per nest varied from zero to ten. There were often additional earth-filled cells from which bees had emerged. In September and October, during and immediately after an unusually dry season, among 32 nests studied, the mean number of new cells or cells occupied by young was only 1.1 per nest, while among the 16 nests with at least one such cell, the mean number was 2.2. By contrast, in January and February, among 27 nests the mean number of such cells per nest was 2.6, and for nests with at least one such cell, the mean number was 3.3 per nest. While these figures are larger than those for *L. seabrai*, they nonetheless suggest protracted reproductive activity, probably associated with the long season of activity. Bursts of activity are evident, perhaps associated with periods of good weather or floral abundance. Thus in one nest there were three eggs and two other cells with pollen but as yet no eggs. Two other nests contained three eggs, three others contained two. Such nests were all found in January and February. Large developmental gaps among the progeny in a nest are not common; in only six of the nests did we find a gap as large as from egg to medium sized or large larva. Nests with two or more eggs usually also contained two or more adults, but the correlation between total number of occupied cells and number of adults in the nest was poor, probably due to death of adults after cell construction and provisioning.

Sociality of females: The number of adult bees in nests examined ranged from one to four. For 40 nests in September and October, the mean number of adults was 1.4, while for 35 nests in January and February, the mean was 1.5. For nests containing at least one cell being provisioned or with immature stages, comparable figures are 1.7 and 2.0. For the five nests in September and October that contained two or more adults, the mean number of adults was 3.0; the comparable figure for January and February was 2.7. Thus the colonies are extremely small but on the average not as small as are those of *L. seabrai.*

Of 20 nests without occupied cells, 13 contained only one bee, the others two. While some of these were associated with old cells and the two bees may have emerged and remained in the nest, others were apparently recently dug burrows, suggesting that after a bee starts a burrow it is sometimes joined by another bee. The conditions of bees in nests without occupied cells are extremely variable—ovarian development D to A, fertilized or not, and mandibles worn or not. One can only conclude that at almost any stage female bees may sometimes be in such nests.

A total of 78 bees were excavated from nests, mostly as complete nest populations. Of these 37.2% were in ovarian Class A (including many lone individuals), 23.1% in B, 16.7% in C and 23.1% in D.

To learn as much as possible about the bees in nests where cells were probably being provisioned and eggs laid, we examined the adult bees in nests with empty new cells or with cells being provisioned, with pollen balls, with eggs, or with young larvae. Dissections of bees from 21 such nests were made. In most cases nests were dug early or late in the day or in cloudy weather so that all adults of the colony should have been present. Otherwise the nests were watched for at least an hour before digging and returning bees captured while bees in the nests were not allowed to escape, so that again all colony members were obtained for most colonies. The data are so diverse that generalizations are difficult; ovarian development, spermathecal contents, and mandibular wear as well as cell contents are therefore indicated for all the bees in the 21 nests, as follows:

1. Sept. 19: A-2, Nol, Dol, Dol; 1 cell with pollen, 2 pupae, old cells.
2. Sept. 19: A+3, Bo2, Co2*; 1 empty cell, 1 egg, 1 *Microsphecodes.*
3. Oct. 11: Co3, Co2; 2 empty cells, 2 medium to large larvae, old cells, 1 *Microsphecodes.*
4. Oct. 26: A-3, Bol, Col; 2 empty cells.
5. Oct. 26: A+1; 1 empty cell.
6. Oct. 26: A+1; 1 cell with pollen.
7. Oct. 27: A+1; 1; 1 cell with pollen.
8. Oct. 28: A+1; 1 cell with pollen.
9. Jan. 31: Bo2; empty cells; 1 cell with pollen, 1 *Microsphecodes.*
10. Jan. 31: A-3, A+2*; 1 small larva, 1 medium larva, 1 *Microsphecodes.*

11. Jan. 31: Bo4, Bo2, Dol; 1 cell with pollen.
12. Feb. 1: A+2, Ao3, Bo3, D+1*, 1 empty cell, 2 with pollen, 1 egg, 1 small larva.
13. Feb. 1: A+2, Co2, D+1*, D-1; 1 cell with pollen, 1 egg, 2 medium to large larvae, 2 pupae.
14. Feb. 1: A+2, A+2, Co2, Dol; 1 cell with pollen, 1 egg, 1 medium larva.
15. Feb. 3: B+2, Co2, 1 cell with pollen.
16. Feb. 6: Ao2, B-2, Dol; 2 empty cells, 2 with pollen, 3 eggs, 1 medium larva.
17. Feb. 6: A-2, Bo2; 1 cell with pollen, 1 egg, 1 prepupa.
18. Feb. 6: A+2, C-2; 1 empty cell, 1 with pollen, 3 eggs, 1 small larva.
19. Feb. 6: A-1, 1 empty cell.
20. Feb. 6: A-4, Bo2; 2 cells with pollen, 2 eggs.
21. Feb. 6: A+2; 1 cell with pollen, 2 eggs, 2 medium larvae, 1 *Microsphecodes*.

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* Guards.

As indicated by Nests 5-9, 19, and 21 above, when there is only one bee in a nest it has enlarged ovaries (usually Class A) and is usually fertilized. Only in Nest 9 (possibly also in 19, where the spermatheca was not found) was the bee unfertilized. For a considerable number of nests (1, 2, 4, 13, 15, 17, 18, and 20) the data can be interpreted as suggesting matrifilial colonies, each with a fertilized queen with enlarged ovaries, usually more worn than the associated worker or workers which are often unfertilized. Nest 16 contained a similar colony but the queen was unfertilized. She therefore was not the mother of the two other adult females in the nest, but must have been a replacement. As in *L. zephyrum*, development of enlarged ovaries like those of a queen does not require fertilization (Michener, Brothers, and Kamm, 1971). Therefore the queens in the other colonies listed above may also have been replacements. In a few nests (10, 11, 12, 14) there were two bees with more or less equally enlarged ovaries. Thus even in these small colonies a queen does not always inhibit ovarian development of her nestmates. Nonetheless, the presence of worn, usually unfertilized bees with only slightly enlarged ovaries (Class C), as in nests 2, 4, 13, 14, 15, and 18, shows the existence of a worker caste. These conclusions are supported by other colonies, not listed above because their brood was all older or cell contents were not recorded.

No significant relationship between size and ovarian class or caste is shown by our material, either when all dissected bees (N = 116) were considered or when populations of individual nests were examined separately. Mean size for Class C individuals was slightly less than for Classes A and B; this is probably not biologically meaningful but since the difference is in the direction expected for a worker caste, the data for head width are summarized here for their possible interest: for ovarian Class A, $\bar{x}$ = 1.44 mm, SD = .069, N = 33; for class B, $\bar{x}$ = 1.45 mm, SD = .074, N = 33; for Class C, $\bar{x}$ = 1.41 mm, SD = .072, N = 31. Bees in a given nest were often of about the same size; often the one with the broadest head in a colony was different from the one with the longest forewing. When distinct size differences existed, the largest bee in the colony was in half the cases not the one with largest ovaries.

As with *L. seabrai* and probably for the same reason, no significant relationship was found between wing wear and ovarian class except that by definition Class D showed no wear. Among 60 bees of ovarian Classes A–C taken as nest populations, there were individuals showing mandibular wear of Classes 1 to 4 in each of the ovarian classes. The mode for mandibular wear in each ovarian class was 2; the mean wear score was not significantly different for Classes A to C. The same was true when all 116 bees were considered.

Spermathecal content demonstrates the existence of a nonmating class of workers. A total of 82 bees were successfully dissected to determine spermathecal content. Of 16 in ovarian Class D, 11 had not mated; clearly at least some mate while young, with threadlike ovaries. Of 21 individuals in ovarian Class C, only one had mated, while of 21 in ovarian Class A, 18 had mated. For ovarian Class B, only 5 of 24 had mated. Of 48 bees in ovarian Classes A to C from nests, 23 had mated and 25 had not. Thus it seems that about half the bees mate. (Bees in Class D will in due course join one of the other classes.)

Among 20 individuals carrying pollen loads as they approached their nests, none were in ovarian Class D, indicating that such bees are not foragers even though some of them do get mated, presumably outside their nests. Two had ovaries of Class A, 10 of Class B, and 8 of Class C. Thus as for *L. seabrai*, over half of the foragers had markedly enlarged ovaries. Spermathecae were successfully examined in 13 of these foragers. Only one had mated. Thus foraging seems to be done largely by unmated individuals, regardless of ovarian size.

Guards were frequently present at nest entrances, so far as we know only at nests inhabited by more than one bee. Guards lunge and bite at natural enemies *(Microsphecodes)*. If sufficiently disturbed by a needle or grass blade they turn and block the entrance with the abdomen. If disturbance continues they often push soil up, into the nest entrance, thus closing it. Thus much of their behavior is similar to that typical of most halictid guards.

The guards from five nests were captured and preserved separately from the rest of the nest populations. They are highly diverse, with ovaries slender or not, spermathecae full or not, and mandibles worn or not. Four of these guards appear in the nests listed above and are marked by asterisks (*).

The sex ratio is often related to the social behavior of females in bees. In view of the very small colonies, one would expect the number of males to be moderately large but at Site A only about one tenth of the pupae were males. This may have been a seasonal and local situation, as females commonly had sperm cells in the spermatheca, and as at Site F, in the five nests studied, about one third of the pupae were males.

Male behavior: Males were rarely found, especially at Site A, although they were more evident at Site F. Only two, one of them still callow, were found in nests. None were seen flying about the nesting areas but at both sites a few were found flying about low plants within a few meters of the nests.

MICROSPHECODES

Two species of *Microsphecodes* were reared from or found as callows in cells of the bees discussed above. *M. truncaticaudus* is a parasite of *Habralictus bimaculatus* and *M. trichommus* is a parasite of *Lasioglossum breedi*. Males and females of the *Microsphecodes* were common, flying around the nesting areas. Mating was not observed but a freshly dead female of *M. trichommus* lying on the soil attracted a male which landed on her and repeatedly attempted to copulate. Thus it seems likely that mating occurs around the nests of the hosts.

At Site A a nesting aggregation of *Habralictus* was in a roadside bank which, at its foot, merged into a horizontal nesting area of *Lasioglossum breedi.* The two *Microsphecodes* species were occasionally intermixed in flight but generally remained separate, each in the principal nesting area of its host. At Site C there was a small group of nests of the *Habralictus* at the edge of a large aggregation of nests of *Caenohalictus eberhardorum.* Here the few *Microsphecodes* were largely limited in their flight to the *Habralictus* area.

Microsphecodes trichommus, mostly females, were frequently taken inside the nests of their hosts *(L. breedi).* Some such individuals may have emerged into the nests but others were in young nests with no cells old enough to serve as a source of adult bees. Therefore, adult females must enter nests of their hosts and once inside, probably stay there for rather long periods to judge by the frequency with which they are found. We have no reason to believe that the situation is different for *M. truncaticaudus;* we dug fewer *Habralictus* nests and therefore have fewer records of its parasite.

Habralictus has no guards at its nest entrances and one sees no females of *M. truncaticaudus* trying to enter host nests, probably because when they find host burrows they can enter promptly. For *M. trichommus* the situation is different for nests of *Lasioglossum breedi* are commonly guarded. We often observed a female of *M. trichommus* on the soil surface facing a nest entrance, head next to the hole and antennae spread, one on each side of the hole. The *Lasioglossum* guard lunged repeatedly at the parasite, which retreated a little at each lunge. On one occasion a guard was able to grasp a leg of the parasite; a struggle ensued, the parasite finally escaping and flying away.

As with related parasites *(Sphecodes* and its relatives, Michener, 1978), female *Microsphecodes* must remove host eggs from cells and replace them with their own, for one never finds a cell with two eggs (host and parasite). In this and other interactions with the host, *M. trichommus* and *truncaticaudus* appear to resemble *M. kathleenae* studied by Eickwort and Eickwort (1972) in Costa Rica.

As noted by Michener (1978), we never saw the *Microsphecodes* on any flowers and suspect that females and possibly both sexes feed in cells of their hosts.

SUMMARY AND DISCUSSION

The bees here discussed fall into three groups: (1) *Habralictus bimaculatus* and *Caenohalictus eberhardorum,* (2) *Lasioglossum seabrai* and *breedi,* and (3) *Microsphecodes trichommus* and *truncaticaudus.*

The two members of group 3 are cleptoparasites in the nests of *L. breedi* and *H. bimaculatus,* respectively.

The members of group 1 nest in aggregations but in individual nests the bees are solitary, communal, or perhaps quasisocial (for definitions see Michener, 1974). The evidence for quasisociality is merely that in each species certain nests contained more bees than there were cells open or being provisioned, implying that the bees cooperate in work on a given cell. Because of the density and structure of nests, however, the chance of observational error is high.

Nests of both species in group 1 have long laterals, each ending in a cell, the nest type being Subtype IIIa, $\bullet(\mathrm{LCh})^n\mathrm{B}$ of Sakagami and Michener (1962). The nests of *Habralictus canaliculatus* and *Caenohalictus curticeps* in Brazil are basically similar (Michener and Lange, 1958; Sakagami and Moure, 1967). Other species of *Caenohalictus,* however, have very different nests with cells organized into a cluster in a cavity, as described for *C. opaciceps* and *rostraticeps* by Claude-Joseph (1926).

Such species should be restudied to determine whether they are congeneric with *C. curticeps* and *eberhardorum.*

The members of group 2 nest in diffuse aggregations. Individual colonies, however, although very small (average of little over two bees), may show division of labor and a eusocial organization. In *L. seabrai* most colonies had a recognizable, fertilized queen and one or two unfertilized workers with some ovarian enlargements like many of those of *L. zephyrum* or *rhytidophorum* (Breed, 1976). These results agree with those obtained for the same species by Michener and Seabra (1959) and Sakagami and Moure (1967). The latter authors report nests with as many as five bees in them (perhaps some were young adults), but the first authors, as in the present study, encountered maximum populations of three. The queens average slightly larger than workers.

In *L. breedi* the usual eusocial organization is less evident. Colonies were about as small as for *L. seabrai;* the largest contained four bees. Some colonies seemed to have a recognizable queen and one or two workers which are usually unfertilized but with some ovarian development. In other colonies, however, there were two queenlike individuals, or an unfertilized queen. No significant size difference between queens and workers was found, an unusual feature shared only with the very different *Lasioglossum marginatum* (Plateaux-Quénu, 1959).

We have no evidence that any of the species studied is inactive at any season of the year. All were active during a severe dry season (September, 1976), at the beginning of the following wet season (October, 1976) and in a period of moderate rainfall (January and February). The species in Group 1 were certainly also active in March, April, May, and June, to judge by specimens netted from the vicinity of the nests. The other species fly less abundantly about the nest sites and only occasional specimens were taken from March to June, but we suspect that they also are active in those months. Probably, therefore, all species can be taken throughout the year in the equable climate of our study area (altitude 2000 m, latitude about 3°30'N).

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RESUMEN

Este estudio ofrece descripciones de los nidos e información sobre los ciclos estacionales y sobre el comportamiento social de cuatro abejas halíctidas, *Habralictus bimaculatus, Caenohalictus eberhardorum, Lasioglossum (Dialictus) seabrai,* y *L. (D.) breedi.* También se incluyen datos sobre dos halíctidos parásitos, ambos del género *Microsphecodes.* Las especies *Habralictus* y *Caenohalictus* nidifican en agregaciones y los nidos individuales son ocupados por una o por varias

abejas. No hay castas y dentro de un nido con dos o más abejas las relaciones son comunales o posiblemente cuasisociales. Las dos especies de *Lasioglossum (Dialictus)* nidifican en agregaciones a menudo disperas y pequeñas. Las colonias tienen un promedio de poco más de dos abejas, y hay reinas y obreras que se diferencian muy poco de las demás, especialmente en *L. seabrai.* Las actividades de las abejas parecen ser iguales durante la estación seca y la lluviosa.

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Fig. 1. View from above of nest of *Habralictus bimaculatus* inhabited by four adult females.

Fig. 2. Views from above of nests of *Caenohalictus eberhardorum,* the upper one inhabited by two, the lower, by three adult females.

Fig. 3. Diagram of flight path of one male of *C. eberhardorum* in its flight area on vertical bank.

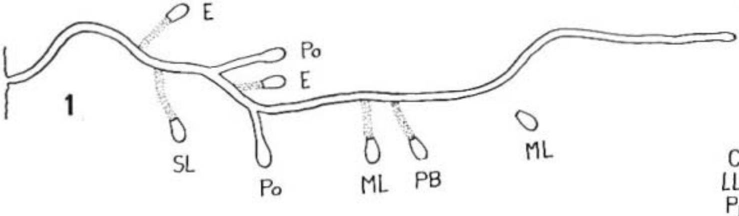
Figs. 4-5. Views from side and above of a nest of *Habralictus bimaculatus* that contained no adult females.

Figs. 6-7. Side views of nests of *Lasioglossum breedi* with three and one adult females, respectively.

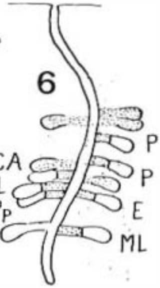
Fig. 8. Side view of nest of *Lasioglossum seabrai* inhabited by one adult female.

Scale lines represent 2 cm, the same for all figures except 3, for which the line represents 10 cm. Cell condition and contents are indicated as follows: R = roughed out, Po = loose pollen, PB = pollen ball, E = egg, SL = small larva, ML = medium-sized larva, LL = large larva, Pp = prepupa, P = pupa, CA = callow adult. Stippled burrows and cells were filled with earth and such burrows are sometimes hypothetical.

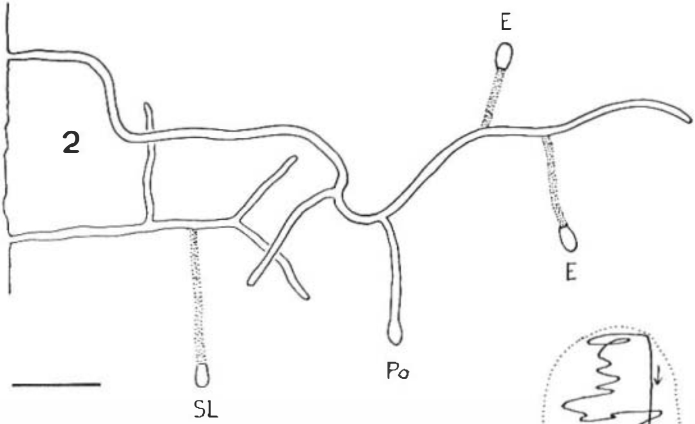
1


E
Po
E
SL
Po
ML
PB
ML

6


P
CA
P
LL
E
Pp
Po
ML

2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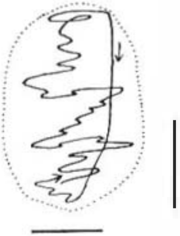
Po
SL

3



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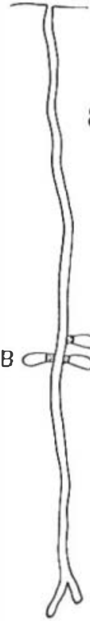
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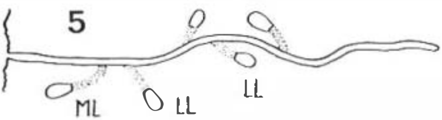
ML

4

5


ML
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ML
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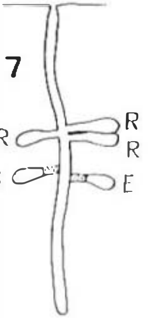
LL

7


R
R
R
PB
E

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