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Geographical Variation in Nesting Biology and Social Organization of *Halictus ligatus*

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**GEOGRAPHICAL VARIATION IN NESTING
BIOLOGY AND SOCIAL ORGANIZATION
OF *HALICTUS LIGATUS***

By

**CHARLES D. MICHENER
and
FRED D. BENNETT**

Vol. 51, No. 7, pp. 233-260

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Geographical Variation in Nesting Biology and Social Organization of *Halictus ligatus*

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ABSTRACT

The halictid bee *Halictus ligatus* ranges from southern Canada to Colombia and Trinidad. In cool, temperate regions it develops small, summer, eusocial colonies similar to those of many halictids and consisting of a queen and several workers which are usually unmated and which lay few if any eggs. These colonies collapse in late summer or autumn, when the old queen and workers die; only new young queens survive the winter. In the tropics and probably also in Florida and elsewhere in the warm temperate regions, while such eusocial colonies may occur as an ontogenetic stage, the colonies become larger and presumably consist of daughters or more remote descendants of the foundress. They are active through all or most of the year and all adult females appear capable of surviving unfavorable seasons. While some of the bees are old foragers, unmated, with slender ovaries, i.e., workers, over half are mated, egg-laying foragers. Most of the eggs are laid by such foragers and in most colonies in these warmer regions there is no evidence of nonforaging reproductives, i.e., queens. The social structure in the tropics does not correspond to any of the named types of social organizations.

There is a continuum in size with no bimodality from the smallest to the largest females. In temperate regions large individuals are produced primarily in late summer and are the young gynes which will overwinter. In the tropics, large individuals are produced at all seasons when there is reproduction. At least some large individuals are produced in large cells with elongate food masses.

Other geographically-varying, biological features are as follows: From Florida southward, males seem to be produced in any months when females are produced. In cool temperate regions, perhaps with the exception of the northernmost population studied (Ontario), males are produced principally in late summer; early summer progeny are nearly all females. Northern populations usually make shallow nests which are often aggregated. From Kansas, southward, nests are commonly deep and rarely aggregated. Nest guarding is common in cool, temperate regions, rare in the tropics.

INTRODUCTION

This paper is an account of the nesting and social biology of a sweat bee, *Halictus ligatus* (Family Halictidae). In most parts of its range this species is common and is presumably a major pollinator, especially of many Compositae. It is important, therefore, that its biology be known, to serve as a basis for its possible future management. The objectives of this study are to make biological information available for this species, to describe a novel type of social organization found in its tropical populations, and to elucidate the geographical variation in social behavior found in this species.

Halictus ligatus is one of the most widespread bees, ranging from southern Canada to northern South America (Fig. 1). At least a little information on nests in burrows in the ground; it falls in the subgenus *Halictus*, but is a distinctive form not closely related to any other species.

The subgenus *Halictus* is largely restricted to temperate regions and has its center of abundance and diversity in Eurasia. *H. ligatus* is the only species of the subgenus occurring in the American tropics and it does not range south of northern South America. For these reasons it seems likely that this species is a recent invader of tropical climates and that attributes of populations in temperate North America are primitive, relative to those of tropical populations. This view is supported by the fact that the social organization in cool temperate areas is similar to that of various other well known halictid bees such as *Lasioglossum imitatum* and *L. zephyrum*. In contrast, the social organization of *H. ligatus* in the tropics is in some features unique among known insects and thus differs considerably from its relatives, including northern populations of the same species.



FIG. 1. Distribution of *Halictus ligatus* with dots indicating the localities where field observations have been made. Areas within the general range where the species does not occur, such as high mountains and deserts, are not indicated.

and seasonal cycles is available from diverse localities, indicated by dots on the map. It is a primitively-social species, usually living in small colonies of females

Halictus ligatus is probably much more abundant, now, in the formerly wooded parts of its range than in primeval times and may have extended its range substantially. Thus, no early collector is known to have obtained it in Trinidad or in South or Central America. Yet in the present century it is common in those areas.

The life cycle and social organization of the species in the temperate region is reviewed in some detail in part I, below. Our data from tropical America are pre-

sented as part II. Part I is the work of the first author and is largely based on the unpublished and published works of others acknowledged therein. Far more than for most papers, we are indebted to the helpfulness and cooperation of these individuals. Part II is a joint work of both authors, based largely on observations made in Trinidad and materials collected there. We are indebted, however, to Drs. M. J. West-Eberhard and W. G. Eberhard for greatly facilitating CDM's brief work in Cali, Colombia.

This paper was made possible by National Science Foundation grant number GB 38502 to the University of Kansas. We wish to acknowledge dissections and

measurements of bees by Kenneth W. Richards, James C. Trager, and Robert E. Gorton, as well as aid in statistical work by the last mentioned. We are especially indebted to Drs. George C. Eickwort and Marcia Litte for reading the manuscript, suggesting improvements, and generously providing information from their own observations.

I. TEMPERATE POPULATIONS

Except for the last subsection, this section is based on populations in the cool, temperate part of eastern North America, i.e., latitude 39° and northward and east of the 96th meridian. Information on populations of cool, temperate regions is from several sources. The first important account of the species concerns populations in the vicinity of Lafayette, Indiana; it is by Chandler (1955), who has given us permission to include material from his unpublished work. It contains many important conclusions about the species, but few data are presented. Chandler apparently made few dissections of bees and no examinations of spermathecae. Parts of Chandler's results were published by Roberts (1973), along with some information from Oregon. Additional material on the Indiana population is included in unpublished work by the late Dr. Rodney Kirkton (1963, 1968).

A series of publications by Knerer and co-authors contains information on *H. ligatus* populations near Toronto, Ontario, Canada, and Kirkton (1968) also provides certain information on the same populations. A comprehensive treatment of the Toronto population has not been provided.

Kirkton (1963, 1968) assembled information about caste differences and geographical variation in *H. ligatus*. His information about nests is not only from Indiana and Ontario, but also from Oaxaca, Mexico.

Litte (in press) made a study near Ithaca, New York, which is very important in clarifying observations made at the other sites. She is the first author to provide appropriate statistical data to document her conclusions.

Near Lawrence, Kansas, one of us (CDM) has made observations on nests of *H. ligatus*, some of them together with H. V. Daly, A. Wille, and E. A. Cross. No major study was made, however, for the nests are sparse. A few of the results appeared in Sakagami and Michener, 1962.

From the sources listed above, the following account of nesting behavior of *H. ligatus* in cool, temperate regions has been assembled; authors' names used without dates refer to the sources cited above. Thereafter an account is given of our limited knowledge of the species in warm, temperate regions.

Nest sites: The nests consist of burrows in gently sloping or flat soil, either bare or with short vegetation, exposing considerable soil. In Indiana, Chandler suggests, nests disappeared from an abandoned garden when weeds became too dense. Nest sites are ordinarily exposed to the sun, but a few of the nests studied in Kansas were partially shaded by trees. Soils are varied, from soft, garden loams or mixed sand and clay to firm silt or hard-packed bare clay paths.

There is a strong tendency for nests to be aggregated. Thus, Chandler reports an aggregation of nearly one hundred nests in Indiana, Litte studied three dense aggregations in New York, and Roberts mentions dense aggregations in Oregon. Kirkton believed that aggregations in Indiana and Ontario, usually on dry hilltops, resulted from limited suitable nesting habitats. Litte, however, believes that the aggregations result from bee behavior, not mere limitation of suitable soils. She notes (*in litt.*) that two aggregations contained 295 nests, an average of 15 nests

TABLE 1. Seasonal Data for *Halictus ligatus* in the Cool Temperate Region, Eastern North America.

Location (North Latitude and Source)	Flight Season	Workers	Males	First Young Gynes	Last Old Queens
N. Dakota (47°) (Stevens, 1951; Kirkton, 1968)	June 18-late Sept.		Aug. 10-? (peak mid Sept.)		
Ontario (43°40') (Knerer and Plateaux-Quénu, 1967a; Kirkton, 1968)	mid May-mid Oct.	late June-early Sept.	late June-early Oct. (peak early Sept.)	mid Aug.	mid July*
New York (42°30') (Litte, in press)	May 8 (or 19)†-Sept. 15 (or Oct. 14)	June 21 (or July 11)-?	July 28 (or 31)-?	Aug. 5	Aug. 31
Indiana (40°30') (Chandler, 1955)	May 3-Oct. 10	June 26-Aug. 29	July 31-Oct. 12	Aug. 10	Aug. 22
Indiana (40°30') (Kirkton, 1968)	late Apr.-mid Oct.		peak mid Aug.		
Kansas (39°) (Kirkton, 1968)	early Apr.-late Sept.		peak mid Aug.		

* One reported in a nest on August 13 (Knerer and Plateaux-Quénu, 1966).

† G. Eickwort (in litt.) reports flight in the warm April of 1976 as early as April 19, but nesting activity did not begin until June.

per m², the mean distance between nearest neighbors being only 14 cm. Solitary nests are also recorded from Indiana, but the large aggregations are striking when compared to sites in Kansas and more southern localities, where nests are usually solitary or in loose groups of only two to ten.

Seasonal activity: Table 1 shows the timing of some major landmarks in the seasonal activity of *H. ligatus* in the northern half of its eastern North American range. The flight season begins with the emergence from the ground of the overwintered gynes and ends with the disappearance into the ground of the new young gynes that will hibernate during the following winter. The column for workers gives the flight season for workers of matrifilial colonies, i.e., daughters of the overwintered gynes which are by now queens. Since workers are short-lived, no one worker lives for the whole period indicated. The first young gynes are the first daughters that will pass the following winter. The last old queens are the last of the overwintered gynes that have lived through the summer as queens. Kirkton's

data are based on museum specimens from squares 270 miles on a side, while data presented by Chandler, Litte, and by Knerer and Plateaux-Quénu are presumably from specific nesting sites.

Nest structure and development: Nests in temperate areas have been described by Chandler, Kirkton, Litte, and Roberts. Sakagami and Michener (1962) also gave data on nests.

In spring, overwintered gynes establish nests by making new burrows, appropriating burrows of the same or other species, or remaining in and refurbishing the overwintering burrows, i.e., the nests of the previous summer. A circular tumulus usually develops; it is much larger at the entrances of new burrows than at those of the other nest types. Such tumuli range up to 5 cm in diameter and over 1 cm high. Similar tumuli are found at nest entrances during the summer, whenever the nests are being extended. Tumuli at entrances of certain nests found in Kansas were highly asymmetrical, fan-shaped, because the upper two or three centimeters of the burrow sloped strongly and tumulus

material was ejected up the sloping burrow rather than symmetrically around a more or less vertical burrow entrance. The burrow entrance is round; Chandler says it is often slightly smaller in diameter than the rest of the burrow, but contrary to that of most Halictinae, often not constricted. In Kansas, however, measurements show entrance diameters of 3 mm, burrow diameters of 5 mm. The soil particles of the tumulus are usually loose and easily blow or wash away, but walls of packed soil, probably consolidated with the aid of a secretion, sometimes extend from the upper part of the burrow up through the tumulus. In such cases, dispersal of the loose material of a tumulus by wind may leave a fragile turret at the nest entrance. The entrance is plugged with soil at night and in inclement weather; indeed, Litte reports that nests inhabited by a single gyne are open for only about 30 minutes per day, while those with multiple foundresses remain open for about six hours.

Below the soil surface the burrows commonly slope slightly, or often considerably in the lower parts where cells are excavated. Thus, cells are commonly attached to portions of burrows sloping as much as 45° . Litte, however, found most burrows that she examined to be vertical. Chandler says that the consolidated lining of the burrow often extends downward, so that only the lower extremities lack it.

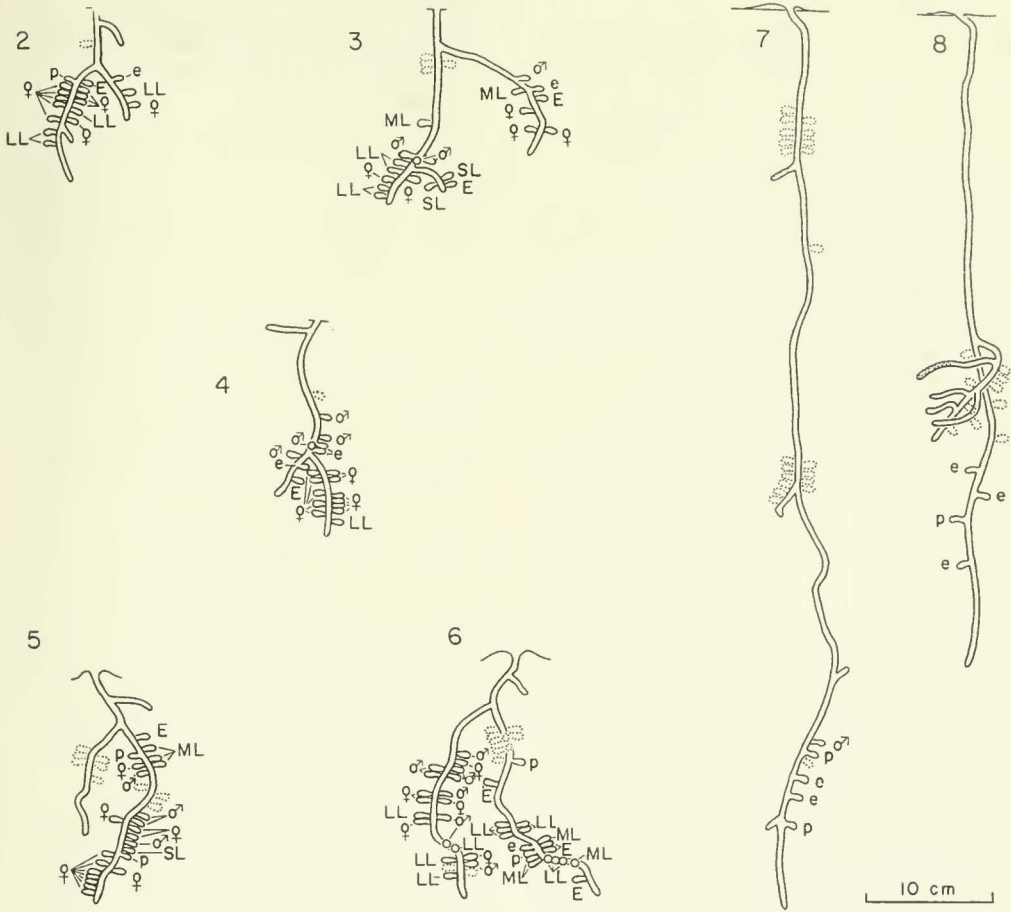
Chandler reports horizontal, lateral burrows 2.5 to 10 cm below the soil surface, each ending in a roughly excavated enlargement (forage cell), in early spring nests. Other authors do not report such features in burrows of this or other halictids and their construction by this bee requires verification. These laterals and cavities are filled with earth before brood cell construction. The spring nest is therefore an unbranched burrow at the time of cell construction and provisioning; Litte reports the average nest depth at this time to be 15 cm and Kirkton says that brood

cells are between 7.5 and 12.5 cm deep. The first completed cell found by Chandler, in different nests in Indiana, occurred from as early as May 15 to as late as June 9.

After a lone overwintered gyne has made and provisioned her brood cells, she closes the nest entrance with earth which fills the upper 3 cm or more of the burrow. She remains in the closed nest until emergence of her first adult workers. In Indiana, Chandler reported that nest closure occurred from June 3 to 14, reopening being on June 26 to 28, or even later. Litte found, however, that nests occupied by two or more overwintered bees do not have a distinct, inactive period between spring and summer phases, such colonies remaining more or less continuously active.

With emergence of daughters, extension of the burrow is begun and this commonly involves branching of the burrow. New cells are mostly along the branches. The maximum number of branches is six. As shown in Figures 2-6, there is often no deep, "main" burrow; below about the level of the bottom of the spring nest or somewhat deeper, branching occurs without a recognizable main axis. Some deep nests in Kansas are still unbranched in August, however (Figs. 7, 8). Perhaps lack of branches characterizes nests in dry soils where great depth is necessary to attain needed humidity.

In Indiana, the cells in summer were less than 25 cm deep, an unsuitable layer of soil being at that depth (Chandler, in Roberts). Such shallow nests, however, appear normal in Indiana, New York, and Ontario. Kirkton says summer nests are 15-30 cm deep, uncommonly in dry summers 45 cm deep, while Litte reports average summer depth as only 18 cm, the cells obviously being even shallower. In a moist region such as the northeastern United States, the cells are probably consistently shallow. As in other halictids, they are deeper when the soil is dry than when it is wet, for they must be con-



Figs. 2-4. Nests from Lafayette, Indiana, June, July 27, and August 13, 1963, respectively; contained three, seven, and eight adult females, respectively (after Kirkton). For explanation of symbols see Figures 15-17.

Figs. 5-6. Nests from Toronto, Ontario, August 11 and 27, respectively; contained ten and fourteen adult females, respectively (after Kirkton). For explanation of symbols see Figures 15-17.

Figs. 7-8. Nests from Lawrence, Kansas, August 29 and 22, 1953, respectively. Each contained four adult females. For explanation of symbols see Figures 15-17.

structed where the soil is moist enough to be workable. Therefore, as summer passes, particularly in dry years, the cells are constructed progressively more deeply.

In Kansas, nests are extended to depths of at least 70 cm in the dry summer months (Sakagami and Michener, 1962). On the basis of few excavated nests, spring cells seem to be at the same depths as in Ontario and Indiana, but in July and August, cells are constructed at depths of 40-65 cm.

Brood cells are of the usual shape for Halictini—horizontal to sloping slightly downward, scattered along the burrows, much as in such *Lasioglossum* as *L. (Dialictus) imitatum* or *versatum* (Michener and Wille, 1961; Michener, 1966). Except for the short necks, they are lined with wax-like material; also, as in most other Halictini.

Worker-producing cells are 9-11 mm long, 5-7 mm in diameter, with the neck joining them to the burrow 1-3 mm long

(Chandler). Chandler reports that in the spring a queen constructs two cells and lines each, then provisions one, then the other. Then she constructs and provisions each subsequent cell before beginning with the next. It seems unlikely that this is a consistent pattern.

As soon as a cell is completed and provisioned and an egg laid in it, it is closed with earth which is so smoothed at the surface of the burrow that the location of the cell is not visible from the burrow. There is no evidence that the cells are opened again until emergence of the adult, although inspection of the young as in *Lasioglossum zephyrum* and other species of *Dialictus* (Michener, 1974, p. 67) may well occur.

Soon after a bee emerges from its cell, the cell is filled with earth. Re-use of old cells has not been recorded and presumably does not occur although new cells may be made in the same vicinity. Chandler notes that cells in which mold develops are somehow recognized in spite of the closed entrances and are packed with soil, a process which pushes moldy material into a mass at the far end of the cell and apparently inhibits fungal proliferation. (Similar behavior is known in *Nomia*; see Batra and Bohart, 1969.)

A lone gyne makes up to six (Chandler) or seven (Litte) cells before closing her nest and awaiting emergence of the first workers. Chandler noted that during one spring in Indiana most gynes made only three cells each, a few up to five; another year when spring weather was better, most nests contained four to six cells before being closed. Litte noted even greater differences between years in New York, mean production being 1.9 *vs.* 4.0 daughters in two different spring seasons. She found nests with two founders sometimes producing more workers, up to 14.

After emergence of the first daughters, cell construction and provisioning go on continuously through the summer. In mid-

September, one of Chandler's nests in Indiana contained 40 cells, including the old, earth-filled ones, and a few other old cells may have been missed in opening the nest. This was the maximum size observed in Chandler's Indiana study. On August 27, a nest illustrated by Kirkton from Indiana contained 50 cells, 12 of them earth filled. These authors give no numerical data but their illustrations suggest that nests often have 15 to 30 cells (including earth filled ones) in August and early September. Litte gives the maximum cell number found among nests in New York as 32 with means of only 10.1 and 6.8 in two different years; these figures do not include old earth-filled cells and thus exclude spring production of daughters.

Although cells in the gyne nests in the spring are constructed in progressive sequence, the shallowest first and subsequent ones progressively deeper, locations of summer cells are often irregular or even retrogressive, so that young of different ages are intermixed.

Cells from which males emerge are similar to those that produce workers, possibly slightly larger in average size; Chandler gives their diameters as 6 to 7 mm, lengths 10 to 11.5 mm. Queen-producing cells, however, are markedly larger according to Chandler, having diameters of 5 to 9 mm ($\bar{X} = 6.5$) and lengths 12 to 17 mm ($\bar{X} = 14$). Reproductives of both sexes are produced from cells irregularly interspersed among worker cells, according to Chandler.

Provisions, as in most other Halictinae, form a smooth, firm, flattened ball on the top of which, in a weak longitudinal depression, a curved egg is laid with its long axis parallel to the long axis of the cell and only its two ends touching the food-mass. Pollen-balls in worker and male-producing cells are reported by Chandler to be about 3 mm wide, 4 mm long and 2 mm deep, but his photographs, in agreement with our Kansas data, show

lengths and widths more nearly equal, the ball being nearly circular as seen from above (see Fig. 9). The pollen-masses in

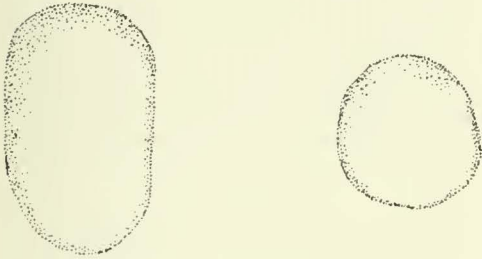


FIG. 9. Pollen-masses from cells from Indiana, traced from photographs by Chandler (1955). Mass from queen producing cell at left, from worker cell at right.

queen-producing cells, however, are not only larger but also elongate, 3.5 mm wide and 5 to 9 mm long (Fig. 9), according to Chandler's text and photographs. No other author reports such a modified cell size and pollen mass shape for queen production in *H. ligatus*, but the parallel with the *Damitas* population of *LasioGLOSSUM (Dialictus) umbripenne* is obvious (Wille and Orozco, 1970). Two pollen masses from a nest in Florida (see below) were large and elongate, however, while another from a different nest was round (G. C. and K. R. Eickwort, unpublished).

The social life cycle: For a short time after nests are first opened in the spring, Chandler, in Indiana, noted that the one to several gynes in a nest come and go, feeding at flowers. It was at this season that he reported construction of the "foraging cells" to which the gynes retreated when disturbed and at night. He reports that brood cell construction does not occur until the foundresses disperse, leaving only one in the parental nest as well as in each new nest. Litte's data from New York appear to support such dispersal, for she found more bees in the early spring nests than later, when brood was being reared, but in different years she found 25 and 32 percent of the nests during brood rear-

ing with two or more bees. Knerer and Plateaux-Quénu (1966) report that in Ontario 60 percent of the spring nests contain more than one (2-7) female. These foundresses, according to the same authors, are not always overwintering groups of sisters, but may contain individuals from other nests. The largest female of a group becomes the queen, the others have less ovarian development and become, in effect, workers or auxiliaries. Litte reached similar conclusions, although in three of eleven two-foundress New York nests, the two females had similar ovarian development. Kansas data on these matters are meager. Of six spring nests found in different places and different years, only one contained two females in mid-May when cells were being provisioned in it.

At least in one nest studied by Knerer and Plateaux-Quénu (1966), a marked auxiliary survived and before dying foraged in early July along with the new workers, thus making an easy transition from a spring, semisocial colony of overwintered mated gynes to the summer, matrifilial, or eusocial colony with a queen and unmated workers. Litte also found in four nests that auxiliaries retained their behavioral roles for at least several days after daughters had emerged and started to forage and two nests opened in August each contained two large, worn, inseminated, foundress-type bees, presumably overwintered gynes; one in each nest had smaller ovaries and was presumably an auxiliary.

In Indiana (Chandler) and New York (Litte) the first brood of offspring, appearing in late June, consists of workers, there being no males until late July. In Ontario, however, according to Knerer and Plateaux-Quénu (1967a), some males are produced in late June, along with the first workers. Under laboratory conditions, the same authors (1967b) found that the monogynous colonies produce principally males, the polygynous colonies, workers.

According to Chandler, male production increases as the season advances, 50 to 75 percent of the cells containing male pupae in the period June 30 to August 14, after which the percentage of male pupae decreases. Adult males leave the nests permanently soon after emergence from the cells. As many as 12 males were found developing in a single nest.

In Indiana (Chandler), New York (Litte), and Ontario (Knerer and Atwood, 1967; Knerer and Plateaux-Quénu, 1967a) worker production continues through much of the summer, the last, newly-constructed worker cells being found about August 1 and the last, active, adult workers on August 29 in Indiana. The length of life of adult workers is so short that colonies never become large. Both Chandler and Litte found that the maximum number of adult workers in a nest at any one time was nine or ten; Litte reports average colony sizes (adult females, including queens) in August of two different years as 4.3 and 3.4 ($N = 25$ and 28 , respectively). Chandler says that 18 to 20 workers in total may be produced by a colony, but presumably less than half of them are usually living adults at any one time. Litte found lower productivity, a maximum for both sexes of 20, with means of only 8.3 and 4.8 in different years. The greatest number of developing workers found in cells of one nest at one time by Chandler was seven.

Overwintered queens may survive through much of the summer (see Table 1, last column). Knerer and Plateaux-Quénu (1966) report excavating a functional, overwintered queen from her nest as late as August 13, although in Ontario most apparently die in July (Knerer and Plateaux-Quénu, 1967a). Litte also indicates considerable mortality of queens during the summer in New York, for 14.3 and 43.8 percent of the nests in July and August, respectively, lacked overwintered queens. Chandler (1955 and in

Roberts, 1973) emphasizes (apparently on the basis of few observations) that if a queen dies, her full function is not taken over by one of the workers, presumably because they are unmated. Instead, they construct some cells, produce male offspring, and the colony dies. This corresponds to the late production of males in Indiana; they were first seen on July 31. Possibly in Ontario, where males develop as early as late June, young females in an orphaned colony may mate, producing replacement queens, and the colony may thus continue more or less normal development. In view of the numbers of colonies reported by Litte to lack overwintered queens, it seems clear that in New York also, replacement queens can be produced. Litte cites two nests in which young were being produced in the absence of overwintered queens. She says, however, that even when the overwintered queens are absent, very few daughters attain fully queenlike ovarian development.

Young gynes first appeared as adults in mid-August, both in Indiana and Ontario. The large brood cells were first constructed in Indiana about July 20 while the last were constructed about August 27. This seems to be slightly later than male cell construction (July 10 to August 22). In New York, Litte found a probable young gyne in a nest on August 5. The number of young gynes produced by colonies in Indiana ranged from 2 to 15, with up to 8 developing in cells of one nest at a time.

The prevalence of gyne and male brood in late summer, failure to produce worker cells in August, and failure of young gynes to contribute to the work of the colony, result in a diminution of nesting (i.e., cell construction and provisioning) activities during August. After the end of that month, the nests are occupied only by young gynes.

Caste differences: There are striking differences in average size between castes,

as shown by the following measurements (mm) of head widths and forewing lengths:

Chandler (Indiana)

Workers:

head widths—2.04-2.68 (\bar{X} =2.34, N=51)

wing length—4.33-5.82 (\bar{X} =5.14, N=50)

Gynes:

head widths—2.42-3.19 (\bar{X} =2.68, N=48)

wing length—4.93-6.79 (\bar{X} =5.88, N=48)

Litte (New York)

Workers:

head widths—2.1-2.7 (\bar{X} =2.49, SE=0.13, N=76)

wing length—5.0-5.9 (\bar{X} =5.50, N=76)

Gynes:

head widths—2.4-3.4 (\bar{X} =2.91, SE=0.19, N=84)

wing length—5.3-7.4 (\bar{X} =6.30; N=84)

Chandler does not indicate the seasons when his samples was taken; Litte's were taken in June and July (daughters), May and June (gynes). The implication of Chandler's work is that there is a recognizable switch from worker production to production of reproductives and that most females can be recognized as to caste by size. Heads of queens seem disproportionately large. In Chandler's data one can see that minimal head width of gynes is larger than mean head width of workers, but minimal wing length of gynes is less than mean wing length of workers. There was probably better differentiation of castes by head width than by wing length.

Examining colonies separately, Chandler and Litte both say that the largest worker is consistently smaller than its own queen. Chandler gives data from eight colonies to demonstrate this. (In one case the wing length of a worker exceeds that of the queen, but other measurements were smaller than those of the queen.)

Knerer and Atwood (1966), in Ontario, found differences in mean size between castes similar to those described by Chandler and Litte, on the basis of measurements of 162 queens and 137 workers. They give no statistical treatment nor data on seasons of capture, but state that workers

become progressively larger during the summer and that there is no abrupt change in size of food masses as production changes from workers to young gynes. Litte implies the same, although she is careful not to jump to the conclusions that the words "workers" and "gynes" imply. She does describe the increasing size of daughters as the summer advances. Probably, there is a continuum from small females (workers) produced early in summer to large females (gynes) produced late.

Kirkton, by means of smoothed curves rather than data, showed bimodality in head width measurements of females throughout the range of the species. He gives no statistical evidence for bimodality, nor do other authors.

To gain further insight into seasonal size variation, head widths of 206 females collected on flowers in the eastern third of Kansas were measured. There is no evidence of bimodality in the whole set of data or for any month. Bees taken in Spring (May) and Autumn (September to November) were lumped as presumed gynes, while each summer month was examined separately, with the following results (mm):

Spring, Autumn (gynes),

1.61-2.94 (\bar{X} =2.58, SE=.023, N=68)

June, 2.23-3.06 (\bar{X} =2.58, SE=.026, N=39)

July, 1.99-2.92 (\bar{X} =2.53, SE=.017, N=72)

August, 2.12-2.67 (\bar{X} =2.41, SE=.027, N=27)

Analysis of variance showed significant heterogeneity among these four means ($P << .001$). A student-Neuman-Keuls test showed the August mean to be significantly smaller than the others ($P << .01$), but no significant differences appear among the other three means. Figure 10 is a histogram showing the frequencies of the various size classes. The relatively large size of the July bees and small size of August bees is a surprise, since one would expect July bees to be mostly workers and August bees to be partly

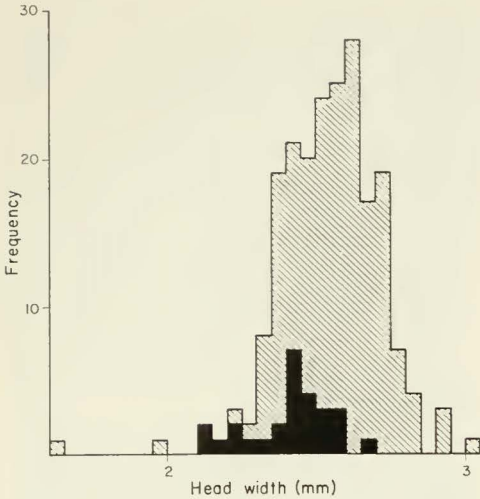


FIG. 10. Histogram showing frequencies of head width classes of females from the eastern third of Kansas. Black represents bees taken in August.

young gynes. Apparently the foraging bees in August, however, are mostly workers, perhaps having matured in July. Samples taken from nests, like those of the authors mentioned above, would probably have been influenced by gynes in August and smaller bees in July. Indeed, there may well be a mixture of castes in our August sample, for the mean head width of the gynes (2.58 mm) is only 7 percent greater than the mean for August bees, compared to 14.5 and 16.9 percent difference in head widths between gynes and daughter workers in Chandler's and Litte's nest populations.

The Kansas data suggest a longer season of activity than in the northeastern localities, with gynes not common away from their nests until September. Perhaps in an area with a long summer season, such as Kansas, the daughter bees on flowers in July, largely reared in June, are larger than the bees produced in mid-summer. This is suggestive of the seasonal size variation found in *Lasioglossum zephyrum* (Batra, 1966; Kamm, 1974) and is in contrast to areas with short summers where the first daughters

produced are perhaps smallest in mean size.

Gynes live as adults for about a year—August or September of one year to July or August of the next. Workers probably survive as adults for only about three weeks, according to estimates by Chandler; Litte observed marked workers for up to 36 days with a mean of 21 ($N = 46$). (Males are estimated by Chandler to survive for two to two and one half months.) Gynes hibernate, but workers do not even live until the advent of cold weather. When nesting alone, gynes commonly go through a quiescent period after provisioning their spring nests; workers are not known to have quiescent periods. After a gyne has reared her first brood of workers, she leaves the nest only occasionally and never brings back pollen for cell provisioning. Chandler reports that even if all workers are removed, such a queen does not revert to cell construction and provisioning. In the absence of the queen, workers often do not fill vacated cells with earth, construct but little, and spend long periods in the nest between provisioning flights.

In the matrifilial, summer nests in Indiana, according to Chandler, the queen with her large head is the usual guard. In a much more detailed study of division of labor, Litte in New York showed that in seven out of eleven nests the principal guard for a colony was the minimal forager, therefore perhaps the queen. This result seems to corroborate Chandler's general statement. In other cases, however, the principal guard was found to be an unseminated worker. Guards bite at potential enemies, but if sufficiently stimulated, turn and close the burrow with the dorsum of the abdomen.

Chandler says that the early-spring, polygynic nests are guarded as in summer, but that during the monogynous period of spring cell-construction and provisioning, the nest is often not guarded.

Knerer and Plateaux-Quénu (1966) and Knerer and Atwood (1967), however, say that spring nests are never guarded, even polygynous ones, a surprising observation, since Litte found spring multifoundress nests to be regularly guarded. Chandler also notes that in autumn, after the workers are dead, the gynes in a nest sometimes guard the entrance.

Litte found that in *H. ligatus*, as in *Lasioglossum zephyrum* (Brothers and Michener, 1974), there is a marked tendency for workers to specialize, some being principal foragers, some being principal guards, and some being less active or doing little. Guards in spring nests averaged larger and had more ovarian development than did principal foragers.

Of course, a prime difference between female castes is in ovarian development. Considering this factor, Litte classified females as follows: A, 5-6 ovarioles enlarged; B, 2-4 ovarioles enlarged; C, one considerably or several slightly enlarged ovarioles; D, all ovarioles slender. The symbols + and o are used to indicate presence or absence of sperm cells in the spermatheca.

All young, adult females are class D; if ovarian enlargement occurs, they join other classes. In spring and summer oviposition periods, egg layers are in classes A+ or B+. In eleven spring nests each with two foundresses, Litte found that the bees ranged from A+ to D+; the foundresses (one from each nest) with most enlarged ovaries had an average ovarian score of 2.6 (A = 3, B = 2, D = 1) while for the other foundresses (workers) the score was 1.7. In three of the nests there was little size difference between ovaries of the two foundresses.

In July and August the ovaries of workers often show some enlargement. Thus, 70 daughters (workers) taken in July and 81 taken in August are distributed as follows in terms of percentages of ovarian classes and fertilization:

	A+	Ao	B+	Bo	C+	Co	D+	Do
July	1.4	4.3	1.4	1.4	0	28.6	2.8	60.0
August	0	3.7	8.6	3.7	0	18.5	8.6	56.8

In New York about 13.7 percent of the daughters (months lumped) have much enlarged ovaries (classes A and B) while a larger number (23.2%), but none of them mated, have limited ovarian enlargement (class C).

Gynes mate readily, but workers are reported by Chandler to be not attractive to males. This presumably is not entirely so, for Litte's data show 5.6 percent of July daughter females and 17.2 percent of August daughter females to be mated.

Overwintering: Mated gynes hibernate in the deeper parts of the nest burrows, presumably in nests in which they matured. Hibernating gynes were found by Chandler at depths of 16-24 cm. The gynes close the burrows behind them with plugs of soil a centimeter or so in length, so that the overwintering cell is a burrow termination or section somewhat longer than the bee. The upper part of the burrow is left open and unattended, but during autumn and winter it is closed by blowing and washing soil.

Warm temperate populations: Few data are available concerning *Halictus ligatus* in the warm temperate areas. Kirkton gives conclusions on the season of activity in all temperate areas, but as they are based on museum specimens, the information may relate to activity of collectors as much as to activity of bees. For the southern half of Florida his maps suggest that the first females appear in late January and that the last females are in the field in late December. It is quite likely that there is no period when flight activity is absent, at least in some years. Mitchell (1960) indicates that there is activity every month and that males were taken on December 18. At the Archbold Biological Station, Lake Placid, Highlands County, Florida, however, Dr. M. Litte (personal communication) found no in-

dividuals of either sex on flowers and found no nests from January to late March, 1975. This was a warm but very dry winter.

Nests found in warm temperate areas, like those in Kansas, have mostly been isolated. G. Eickwort (*in litt.*) suggests that humid conditions of soil may be important in determining nest distribution or survival, for the nests he found in Florida at the end of the dry season were either where they received drainage from a shed roof or along the banks of a drainage canal. Also, in southern New Mexico, 51 km south of Animas, near a water hole where the soil was moist, he found a large, dense, nest-aggregation similar to those in the northern part of the range.

Data on two nests from the Archbold Biological Station have kindly been made available by Drs. George C. and Kathleen R. Eickwort. The nests, opened on April 24, 1972, were in sandy soil, nearly vertical, 86 and 170 cm deep, and did not differ in form from other deep nests of the species, such as those from Kansas (Fig. 11). The bees in this region, like those in the tropics, are large and the burrows were 6-9 mm in diameter (mostly 6.5-7). One had a tumulus 7.5 cm in diameter. The two nests contained 16 and 23 cells and 4 and 7 adult females, respectively. One cell and an earth-filled old cell were found at a depth of 21 cm, but otherwise the cells were located from 48 to 160 cm in depth. They contained young of all stages, including male pupae.

The Eickworts' observations verify Chandler's report of some elongate pollen masses, no doubt producing large bees (gynes?). They measured one round pollen mass (5×5 mm \times 3 mm high) and two elongate ones (9×5 mm, 4 mm high).

In each nest the largest bee was mated and had much enlarged ovaries (class A) and in the deeper nest this individual was

also much worn. One or two other individuals in each nest also were mated and with enlarged ovaries (our class A or B). The unmated individuals had ovaries of classes B and C, except for one in class D, and were not or were little worn.

The large number of mated bees with enlarged ovaries is suggestive of the tropical populations. This similarity is strongly supported by 17 females taken on flowers by Dr. G. C. Eickwort at Lake Okechobee and 23 miles southwest of Clewiston, Florida, April 5 and 11, 1974. All these foragers, which were dissected by Dr. Eickwort, were mated and eight had at least somewhat enlarged ovaries, probably falling in our classes B and C. Of course, these bees could have all been queens, but this was not suggested by their size nor by the populations of the two nests found at the Archbold Biological Station, which is in the same general area.

The only two bees taken in a nest in red volcanic soil 12 miles southwest of Apache, Arizona, August 16, 1972, and dissected by Dr. G. C. Eickwort, were mated, with enlarged ovaries. This nest was only 35 cm deep and contained but one active cell in addition to old, earth-filled cells and a dead female.

From these meagre data, it seems probable that during the long flight seasons in warm temperate areas, colonies like those of the tropics develop.

II. TROPICAL POPULATIONS

Information on tropical populations has been obtained in several areas. The bulk of the data were obtained at Curepe, Trinidad, West Indies ($10^{\circ}40'N$) by Bennett and Michener. Limited amounts of information, however, were gathered at Cali, Colombia ($3^{\circ}30'N$) and 5 km north of Chame, Panama ($8^{\circ}30'N$) by Michener, at Turrialba, Costa Rica ($9^{\circ}40'N$) by

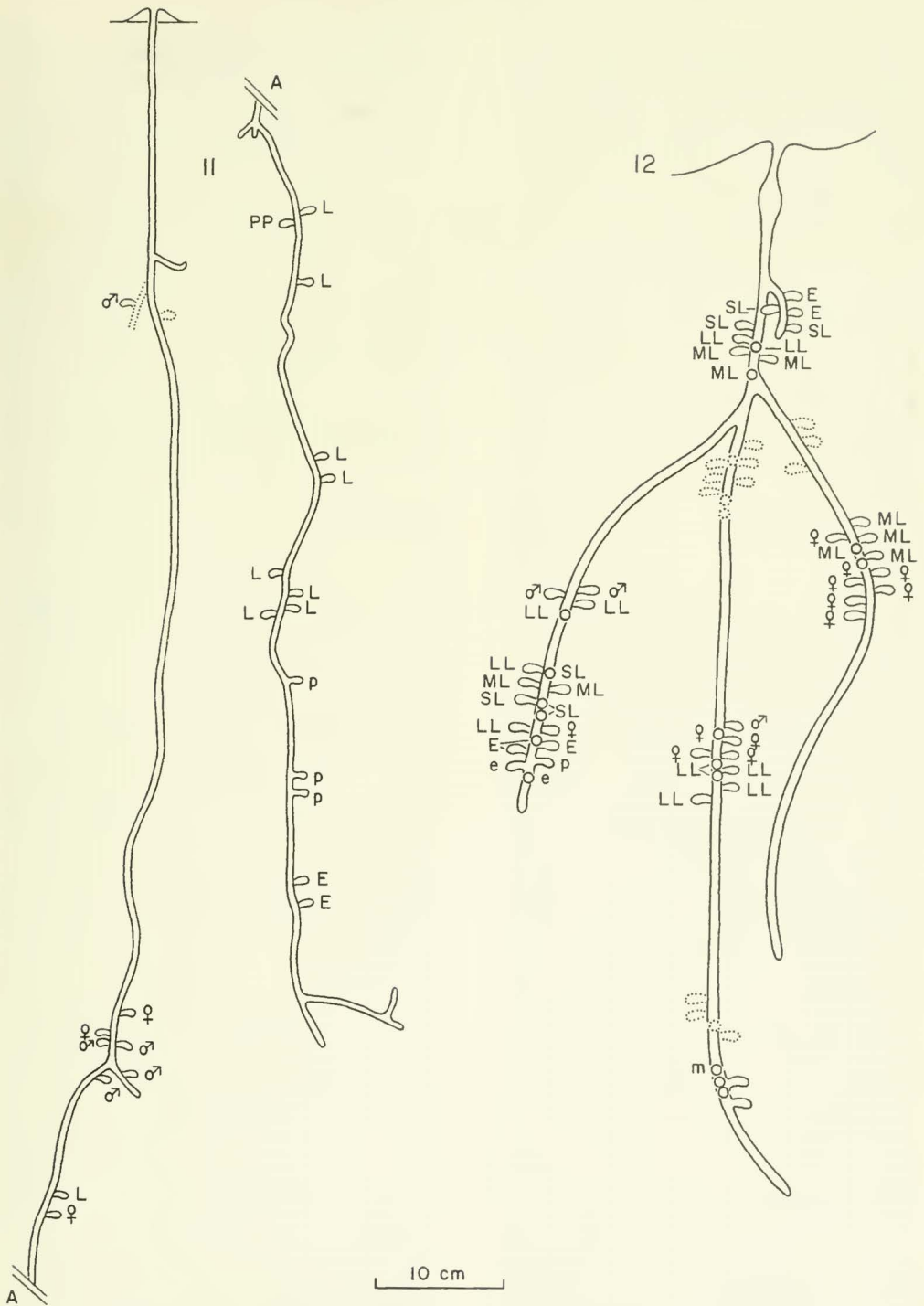


FIG. 11. Nest from Archbold Biological Station, Lake Placid, Florida, April 24, 1974; contained seven adult females (from field notes by G. C. and K. R. Eickwort).

FIG. 12. Nests from Mitla, Oaxaca, Mexico, July 5, 1965; contained eleven adult females (after Kirkton).
For explanation of symbols, see Figures 15-17.

Drs. George C. and Kathleen R. Eickwort (unpublished) and 9 km east of Tehuantepec (16°20'N) and at Mitla (16°50'N), both in Oaxaca, Mexico, by Kirkton (1968). The more southern of these sites approximate the southernmost known localities for the species, both in the west (Colombia) and in the east (Trinidad) (Fig. 1).

Methods: To roughly monitor seasonal abundance on flowers and to obtain material for studies of any seasonal changes in bee size, ovarian development, wear, frequency of mating, and the like, "special collections" were made at intervals through three years in the general vicinity of the nesting site at Curepe, Trinidad. They were made by walking in mid-morning along roadside patches of *Bidens pilosa*, which fortunately blooms throughout the year, capturing as many *Halictus* as practical in a period of about an hour. For some lots bees that had collected pollen loads on the scopae were kept separate from those that did not have large scopal loads. Except in January, 1972, the special collections were made by FDB.

The nests at Curepe were watched casually over a period of years by FDB. Some of these nests, as well as those at Cali, Colombia, were excavated by CDM, using in general the techniques described by Michener et al. (1955). Burrows, however, were marked by blowing powder from a plastic squeeze bottle into them instead of by pouring in plaster of Paris.

Before opening it, each Trinidad nest was watched for an hour or more and all returning bees captured. Departing bees were allowed to go, but captured on their return. Thus, all individuals active in the field at the time were caught and kept segregated from bees remaining in the nest, which we call "nest bees." Of course, some of these nest bees might well leave the nest at another time. Bees returning with pollen loads were also sep-

arated from the rest for study. The expression "bees associated with nests" is used for the nest bees plus foragers taken as they returned to nests, 62 in all. For statistical purposes "foragers" are the bees taken in special collections plus those that were returning to nests, 383 in all.

Bees from the nests as well as from special collections were preserved in Dietrich's (Kahle's) fixative and were measured and dissected later, using the techniques described by Michener et al. (1955). Head-width was used as the measure of size, although forewing-length was also taken. Mandibular wear was coded one (unworn) to five (worn down to subapical mandibular tooth). Alar wear was recorded as the number of nicks in the apical margin of each forewing. An index of wear for each bee was obtained by adding its mandibular code number to the average number of nicks on the two forewings; a freshly emerged bee has an index of wear of 1. Bees were regarded as mated if the spermatheca contained sperm cells; otherwise they were considered unmated. The ovaries of each bee were sketched and maximum ovarian width and length of the longest oocyte were also recorded. Some of the drawings were sent to Dr. Marcia Litte who classified them according to the system summarized in Part I above. Not all ovarioles were visible in the drawings, but she was confident of the categories. We are thus able to use, in addition to the measurements, lettered categories equivalent to hers.

Nest sites: The site in Trinidad, which was active for at least six years, was near houses on a hill just north of Curepe. The nests were in soil consisting of decomposed shale near the surface that could be cut with a knife, the soil being harder and with solid rocky regions at depths of 70 to 90 cm. The site was almost level, covered with coarse vegetation that was usually clipped short. The nests survived

a period of two months when the uncut grasses and weeds grew to a height of about 30 cm, but disappeared ultimately, possibly because vegetation was allowed to grow for a longer period. Six nests were found in an area of about one square meter. There were a few scattered nests nearby and there must have been many in the general area, for the bees were common on flowers of *Bidens pilosa* and *Melanthera nivea*, both weedy Compositae. Pollen loads from each plant (distinguishable by color) which were carried into the nests indicated that *Bidens* was more often visited than *Melanthera*. Nests were excavated in late December, 1971, and January, 1972; otherwise the population was kept track of by monthly samples from the *Bidens* flowers. Three isolated nests near Turrialba, Costa Rica, were also in level ground with grasses and herbs.

Near Cali, Colombia, and Chame, Panama, nests were found in the very hard, bare soil of foot paths. The soil surface was flat or gently sloping. Most of the nests were isolated although three were about 20 cm apart. Kirkton's three nests from Oaxaca were all isolated.

At no tropical site have we encountered dense nest-aggregations like those in Indiana, New York, and Ontario. Dr. Alvaro Wille of the Universidad de Costa Rica, however, has told us of a site near San Mateo, Costa Rica, inhabited by a moderately dense aggregation.

Seasonal activity: This section is based entirely on data from Trinidad, although seasonal activity at other tropical locations is presumably similar. Nests excavated in January in Colombia appeared to be in the same condition as those excavated at the same time of year in Trinidad and, in fact, nests excavated in July in Costa Rica and Oaxaca were also similar.

To understand the bee's seasonal activity, it is necessary to have information on the seasonal cycle itself. Weather data are from the University of the West In-

dies, St. Augustine, about 3 km from the nesting site. Temperatures are warm and rather uniform throughout the year. Monthly mean minima during the years 1972-1975 ranged from 19° to 23° C (67° to 74° F), with a tendency for lower mean minima during the Northern Hemisphere winter and spring months. Monthly mean maxima ranged from 29° to 33° C (84° to 91° F), again with a tendency for lower means in the Northern Hemisphere winter and spring months.

Rainfall occurs in every month of the year with a total annual rainfall of 1200 to 1475 mm (48 to 59 inches). The dry season, with 3 to 75 mm (0.12 to 3 inches) of rainfall per month, usually extends from January through May, in some years beginning in December or extending through June. Sometimes (e.g., 1972) January and May are wet so that the dry season is only February through April. The wet season, with a monthly rainfall of about 100 to 300 mm (4 to 12 inches), occupies the rest of the year.

Data on seasonal activity in Trinidad are based largely on the special collections made from flowers at Curepe, but, in part, on dates of capture of specimens in the collection of the Commonwealth Institute of Biological Control in Curepe. These collections were somewhat irregularly distributed, but, over three years, one or more special collection was made or attempted in each month except November.

Halictus ligatus has been taken on flowers at Curepe in every month except May and November. In November, although no special collections were attempted, there is good reason (abundance in late October and early December) to believe that activity continues uninterrupted. In most months, a special collection, such as is described above, resulted in capture of 25 to 38 female *Halictus*. Three different collections in April, however, produced 5, 1, and 4 bees each. In May, none were taken and in

June only two. The collection of the Commonwealth Institute of Biological Control contains 13 taken in April, none in May and two in June.

From these data, it seems that there is a period at the end of the dry season and perhaps continuing into the beginning of the wet when the species is scarce on flowers. There is no obviously competing flower that might account for its disappearance from *Bidens* at that time. The special collections in April to June were all made or attempted in 1974, a year in which the dry season continued through June, the rainfall that month being only 2.33 inches.

In July, there is the same mixture of fresh and worn bees as in any other month. Thus, if adults of mixed ages become relatively inactive in April to June, they probably emerge and resume work after the rainy season begins. It is possible that after a long dry season the soil is too dry to make cells and the bees become inactive until it is workable again.

Males have been taken at Curepe in January, March, July, August, September and December and probably are active whenever females are to be found.

Large females, suggestive of north temperate gynes, but even larger (workers, also, are larger in the tropics than northern workers), occur in the tropics. As explained later, however, such individuals are not always gynes. In Panama and Oaxaca three such individuals were found, apparently starting new nests, in June and July. By itself, this is not evidence that nest establishment is highly seasonal, but it might occur predominantly at the beginning of the wet season when activity resumes. Colonies in large nests can also be found in July (Costa Rica, Oaxaca), suggesting that they do not break down in the inactive season as do colonies in the cool temperate autumn. The months of capture on flowers of the largest 10 percent of the females taken in Trinidad

are January, March, April, August, September, October, December. Thus, large females can probably be found on flowers whenever other females are there. The largest female taken at Curepe, markedly larger than any other, was on flowers in October. Fresh and unworn, it could not have started a nest in June or July.

Nest structure and development: Three apparently new nests, shallow burrows each occupied by one large female with no cells or with a cell or two roughed out, have been found by CDM in Panama in early July and by Kirkton in Oaxaca in June. If new nests are started primarily by large, unworn females, as seems possible in view of the situation in a temperate climate, it may be significant that essentially unworn, large females (head width over 3.5 mm) have been taken in Trinidad in January, March, July, September, and October, four of them in the latter month. New nests were not found in Trinidad, despite a search in December and January and general surveillance throughout various years.

The nests studied in Trinidad and Colombia in December and January are the bases for the following account, with parenthetical comments for other regions. The nests were much larger than those in the northeastern parts of the range. Tumuli of fresh soil up to 9 cm in diameter (Fig. 13) were found, showing extensive



FIG. 13. Nest entrance at Curepe, Trinidad, showing large, fresh tumulus. The numbers represent inches (2.5 cm = 1 inch).

digging in some nests in December and January. Old tumular material, packed and washed by rain and sometimes with grass growing in it, but recognizable by the color of the subsoil, was also evident around many of the nests.

Measurements of entrances and burrows are slightly larger than for those in Kansas, entrances being 3.5 to 5 mm in diameter, burrows 5.5 to 6 mm. Nothing suggestive of a turret was seen at any time, nor were nest-entrances ever seen closed by soil, except sometimes by fresh tumulus material being pushed out. There was no evidence of regular nocturnal closure, as is reported in the north. Although part-time guarding occurred early in the morning, and the sun was often on the nest sites, flights from the nests did not begin until about 9:30 a.m. Rain or threatened rain usually stopped activity in the early afternoon.

While the nests were much deeper than in the north, the number of branches was not greater (Figs. 12, 15-17), the mean for six nests being 4.4 and the maximum being 6. The distribution of earth-filled, abandoned cells showed that there had been other branches at depths from 15 to 60 cm, but they had evidently been filled and abandoned at earlier stages in nest-development. Presumably, the number of branches remains more or less constant, old ones being filled as new ones are made.

The deepest nest (Trinidad) was 97 cm deep, the shallowest (Colombia), 79 cm (Costa Rica, 55 cm). The burrow walls are often lined 0.5 to 1.0 mm thick with soil from deep in the nest (as shown by color), bearing the marks made by tamping with the apex of the abdomen. Chandler's report of a consolidated soil lining is thus verified (as also in Arizona and Florida nests excavated by the Eickworts). The tendency of burrows to slant, often in a single direction, is prominent in Trinidad (and Costa Rica) (Figs. 15-17). The bottoms of some nests in Trini-

dad were offset 60 cm or more horizontally from the entrance. In Colombia and Oaxaca, the burrows were nearly vertical.

Many earth-filled, old cells, mostly with feces, indicating probable survival and emergence of the occupants, showed that the colonies had been active for considerable periods, months and possibly years, prior to our digging of them. In Trinidad the shallowest earth-filled cells found were 18 cm deep; in Colombia, 15 cm. This may be the depth at which nest foundresses make cells, but, if so, the nests were perhaps established by multiple foundresses, as there were many old cells at these depths.

The uppermost, occupied cells found were 27 cm deep, both in Trinidad and Colombia (9 cm in Costa Rica); the deepest were 95 cm (19 in Costa Rica). They were often intermixed with earth-filled cells and young of different ages were often intermixed. Nonetheless, in general, eggs and younger brood were deeper in the nests than pupae. In six Trinidad nests with a total of 161 occupied cells, 82 percent of the 61 cells less than 70 cm in depth contained pupae and only 7 percent contained eggs or feeding larvae. For the 100 cells over 70 cm deep, the figures are 51 percent for pupae and 37 percent for eggs and feeding larvae.

The tendency of the tropical nests to be very deep, despite humid climate, is interesting, since in Europe and North America (Michener and Wille, 1961) halictid nests are deeper in dry than in humid seasons. Perhaps soil temperature is also important in influencing nest-depth. It is also true that the heat of the tropical sun tends to dry the soil more in a given time than the same period of sunshine in the north. In both Colombia and Trinidad, the surface soil seemed rather dry much of the time in January, despite frequent rains.

All cells (Fig. 14) found in the tropics correspond to Chandler's male-and-work-

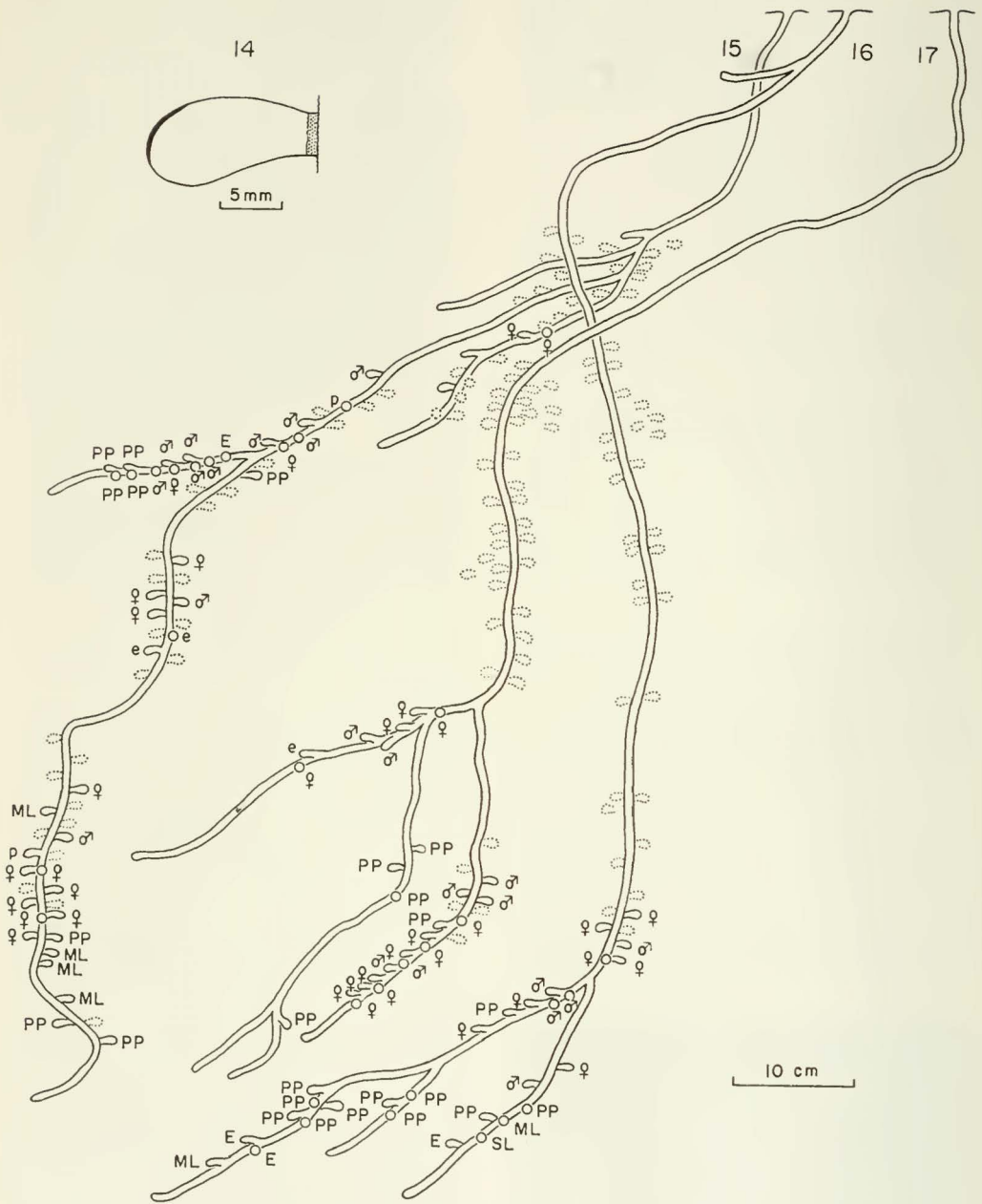


FIG. 14. Cell from Curepe, Trinidad. Black represents larval feces.

FIGS. 15-17. Nests from Curepe, Trinidad, December, 1971, and January, 1972; contained 14, 16, and 12 adult females, respectively. The symbols used in these and other illustrations of nests are as follows: Dotted cell = earth-filled, abandoned cell; m = moldy; P = pollen in open cell, being provisioned; e = empty, adult recently emerged; E = egg; SL = small larva; ML = medium-sized larva; PP = large larva, usually prepupa; ♂ ♀ = pupae of the sex indicated.

er-producing cells. The southern bees are somewhat larger, hence measurements are in general a little longer, as follows: Cell length (including the neck) 12 to 20 mm (Chandler's measurements apparently did not include the neck); diameter 6 to 7 mm; diameter of neck 3.5 mm. The cell-closure was usually about 1 mm thick and most cells were 14 to 15 mm long including the neck or closure. Sometimes there was a small irregular hole in the closure. This might result if some of the loose soil fell out, but did not seem to be a result of the investigator's work.

The number of occupied cells per nest from six nests in Trinidad ranged from 18 to 44 ($\bar{X} = 34$) (11 in Costa Rica). Earth-filled cells were at least as numerous and probably more so; counts were difficult to make and were not seriously attempted. This mean is enormously greater than means for Litte's nests in New York, but the maxima are in the same range.

Food-masses were shaped like those in Chandler's worker-and-male-producing cells, but were slightly larger, $4.5 \times 4.5 \times 2.8$ mm, the last being the vertical measurement.

Colony size: Colonies in the tropics are markedly larger than those in the cool temperate regions and those excavated were not obviously eusocial, but seemed more nearly communal (terminology of Michener, 1974). Eleven tropical colonies have been partially or fully examined. The smallest which was excavated was from Costa Rica, with only four females (one from Trinidad had only one foraging bee and at least one other bee in the nest, but was not excavated). The largest colony fully studied was from Trinidad; it contained 16 females. Another, from Colombia, contained 11 foraging bees and an estimated 21 in total. In six fully-excavated, tropical nests, three opened in June and July in Costa Rica and Oaxaca, three in Decem-

ber and January in Trinidad, the mean number of females was 11.3.

Immature stages: The nests studied in Trinidad in December and January, Colombia in January, Costa Rica in July, and Oaxaca in July contained immatures of all stages. The climatic regimes in these areas are reasonably similar and production of young of both sexes is presumably continuous with the probable exception of the brief period when adults disappear from flowers (in Trinidad).

Guards: In Trinidad and Colombia guards were sometimes seen at the nest entrances. They are inconspicuous compared to those in northern, summer colonies and in many cases an apparent guard may be only a bee about to leave the nest. Usually, they retreat when disturbed, but one turned and blocked the nest entrance with her abdomen. Four guards were collected and subsequently measured and dissected. From this small sample no suggestion of consistent size or internal differences between guards and foragers was detected. The guards were of moderate size, little to considerably worn, mated or unmated, with varying amounts of ovarian enlargement.

Bees associated with nests: Data are available on 62 bees associated with nests in Trinidad. Except for one, possible nest-foundress and one or two possible, potential foundresses (large young bees), this sample is a reasonable tropical counterpart for Litte's sample of daughter bees from nests in New York. Data are presented in Table 2. The following features are worthy of comment: (a) Frequency of mated bees, amounting to 58.1 percent of all bees. (b) Existence of some worn, unmated bees. (c) Absence of bees with ovaries of class A (fully enlarged). (d) Abundance of bees with moderately enlarged ovaries (class B), amounting to 51.6 percent of the individuals, mostly mated. (e) Lesser abundance of individuals in ovarian class C, amounting to 38.7 percent, mostly un-

mated. (f) Scarcity of individuals with slender ovaries (class D), amounting to only 9.7 percent, mostly unworn and all unmated. The contrast with Litte's data is striking, as noted in the Discussion below. The mean size of bees associated with nests did not differ significantly from that of foragers.

For the few Trinidad nests which were completely excavated with all inhabitants captured, 47.5 percent of the 40 females were taken at the nest-entrances, returning with pollen. Pollen-collecting individuals have approximately the same mean head-width and variance thereof as do all females from Trinidad. Of the pollen-collectors, 63.8 percent were fertilized. They ranged from unworn to the most worn of all the individuals taken at the nests; nearly half had indices of wear less than 5. Nearly all showed some ovarian enlargement (classes B or C), although 3.2 percent of the pollen-collectors have ovaries placed in class D. Among pollen-collectors, 23.7 percent had an oocyte 2.0 mm long or longer, often apparently nearly ready to lay; such bees were all fertilized. Not a single nest-bee, including the most queenlike individual, contained an oocyte approaching 2 mm in length. Thus, it seems that the foragers are the principal reproductives, as in solitary bees.

It is clear, however, that not all the bees mate and lay eggs. Of the bees associated with nests, about one third had an index of wear of 5 or more and were therefore presumably the older individuals; of these 33.3 percent were not fertilized and had ovaries of classes C or D. Thus, about one sixth of the bees are apparently non-reproductive workers. Such individuals are not always small bees, but at least among foragers there was a significant, positive relationship among ovarian-width, mating, and head-width, suggesting that larger bees are more likely to become reproduc-

tive than smaller ones. (For details see material below on Foragers.)

Of the nest-bees (taken in the nests), over half were unmated, mostly with indices of wear of 1 or 2. Although such bees are presumably young adults that have foraged little if at all, some showed some ovarian enlargement (class C). Nest-bees showed a size-range and mean size essentially the same as those taken (nearly all carrying pollen) as they returned to their nests and as foragers in general.

Foragers: To elucidate the attributes of foraging bees, all the females taken in Trinidad in the special collections from flowers were measured and dissected. Nearly all these bees were collecting pollen. The few that had little or no pollen on the scopa were in no other way different from those that were collecting pollen. Hence, all are termed foragers and were analyzed together with the foragers caught returning to nests with pollen, making a total of 383 females. Head-widths of the specimens from Curepe, Trinidad, in the collection of the Commonwealth Institute of Biological Control were also measured, thus providing size data on 147 additional females.

The most noteworthy attribute of the foragers is the high percentage that have enlarged ovaries and are mated. Data on these features are shown in Table 2, and support, with some modifications, the comments on bees associated with nests, as follows: (a) Mated foragers, 55.6 percent of total, only slightly more numerous among worn than among little worn and presumably younger bees. (b) Existence of worn, unmated bees. (c) Small numbers of bees with ovaries in class A. (d) Abundance of bees with moderately enlarged (class B) ovaries, totaling 49.9 percent, the great majority mated. (e) Abundance of bees with less developed ovaries (class C), amounting to 45.4 percent, mostly unmated. (f) Scarcity of individuals

TABLE 2. Percentages of insemination (+, o) and ovarian classes (A-D) in bees from Curepe, Trinidad.

	Index of									N
	Wear	A+	Ao	B+	Bo	C+	Co	D+	Do	
Associated with nests	< 5	36.8	7.3	17.1	26.8	12.2	41
	≥ 5	66.6	28.6	4.8	21
Foragers	< 5	4.1	41.0	8.5	10.0	35.8	0.7	271
	≥ 5	0.9	46.4	4.5	9.8	34.8	3.6	112

with slender ovaries (class D), only 1.5 percent, mostly worn, all unmated.

An analysis of variance demonstrated no significant heterogeneity among bi-monthly means of head-widths. Thus, no seasonal size variation is recognizable. The frequencies of head-widths among all females from Trinidad are shown in Figure 18.

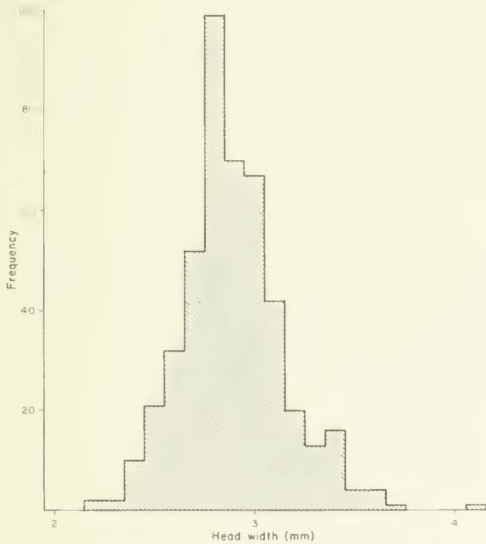


FIG. 18. Histogram showing frequencies of head-width classes of females from Curepe, Trinidad.

There is a general positive relation between size and insemination, so that the larger bees are more likely to be inseminated. Thus, of those whose spermathecae were examined, 51.4 percent of the 140 below the modal head-width were unmated while only 37.7 percent of the 159 above the modal head-width were unmated; the mean head-width of mated

bees was significantly larger than that of unmated bees ($p << .001$). Nonetheless, both mated and unmated bees were widely scattered across the size range. Although the two smallest bees in the study were unmated, the third in size was mated. At the other end of the size scale, the largest of all the bees was unmated.

Large bees are also more likely to have considerably enlarged ovaries than small bees. There is a positive correlation ($r = .273, p < .01$) between ovarian width and head-width, and a similar but weaker correlation ($r = .205, p < .01$) between length of the longest oocyte and head-width. These relationships are not entirely a result of the limited space available for ovaries in small bees, as shown by the large ovaries of the smallest of all our dissected bees. Its longest oocyte was longer than average (1.53 mm), while at .71 mm in maximal ovarian width, only 7.6 percent of the bees had wider ovaries. (Not surprisingly, there is a strong correlation, $r = .729, p << .01$, between ovarian width and length of the largest oocyte.)

Since there are positive relationships between head-width and the percentage that have mated and between head-width and ovarian width, it is not surprising that there is also a strong positive relationship between ovarian width and mating, maximum ovarian width of mated females being greater than that of unmated ones ($p << .001$). Mean ovarian width of mated foragers is 0.59 mm, of unmated ones, 0.40 mm. There is no significant correlation ($r = .003$) between the index

of wear and ovarian width; there are some extremely worn bees with slender ovaries and little-worn bees with strongly enlarged ovaries.

Probably, there is no meaningful relationship between mating and subsequent survival and work. Among 243 females with an index of wear of less than 7, 42.8 percent were not mated. Among the 55 females with an index of wear of 7 or more, 50.9 percent were unmated. Thus, one might suspect that unmated bees work harder, live longer, or visit flowers more when old, than do mated bees. The difference is neither great nor statistically significant, however. Among the 21 most worn bees there are both unmated and mated individuals at the frequencies of 11:10. Thus, there is no consistent evidence of a progressive change in the ratio of mated to unmated bees as the bees pass from unworn to much worn. This suggests that females mate when young or not at all.

There is a weak indication that larger bees tend to work more or longer than smaller ones, the correlation coefficient between head-width and wear being $r = .163$ ($p < .01$). However, the 45 bees whose indices of wear were 9 or above had almost exactly the same mean size as did all the bees from the special collections. The second and third largest bees in the study were much worn, with indices of wear above 15.

Table 3 summarizes the relationships described above.

Large bees: In cool, temperate climates, the overwintering gynes that establish nests in the spring and remain as queens through at least part of the summer are large as compared to the summer daughters, which are here called workers. A small percentage of the tropical females seem to be similarly large, and special attention to them seems worthwhile. Examining the largest 10 percent of the 403 dissected females from Trinidad and Colom-

TABLE 3. Relations among attributes of females of *Halictus ligatus* from Curepe, Trinidad. The upper right represents individuals associated with nests in December, 1971, and January, 1972. The lower left represents foragers (mostly pollen collectors, hence the blank lower row) taken throughout the year. The numbers of the columns correspond to the numbers of the rows. + = a positive relationship; 0 = no significant relationship.

	1	2	3	4	5
1. Head width	+	+	0	0
2. Ovarian width	+	+	0	+
3. Insemination	+	+	0	+
4. Wing wear	+?	0	0	0
5. Pollen collecting

bia, we find unworn or nearly unworn individuals (indices of wear 1 and 2) among those taken in January, March, April, July, August, September, October, and December. Thus, large females seem to be produced in small numbers throughout the year. Much-worn, large individuals also occur throughout the year.

As is to be expected from the preceding subsection, most of the 40 large bees are mated and have enlarged ovaries, although the ovaries are not strikingly larger than those of many smaller bees. Of nine that were unmated, six were unworn and even though on flowers, some of them carrying pollen-loads, they would probably ultimately mate. The remaining three, unmated and worn, collecting pollen, including some of the largest bees in the study, show that not all large bees become reproductives. Most large bees, however, are more reproductive than most small bees: 31 of the 40 large bees had ovaries at or above the median ovarian width and 14 had an oocyte 2.0 mm long or longer. In terms of ovarian classes, 4 large females were in A, 27 in B, and 9 in C.

Since the only three tropical nests that have been seen early in establishment contained a lone large bee, and also in con-

formity with observations in the north, it seems probable that a nest is usually started by a large bee.

One nest excavated in Trinidad still contained a possible foundress, here hesitantly called a queen (head-width 3.63 mm, mated, index of wear 9, ovaries of type A with maximum width .81 mm). She was larger than any other bee in the nest except a fresh young adult of the same size, mated, but with rather slender ovaries (maximum width .30 mm). In addition to the queen, the colony contained seven foragers and four other bees that were in the nest, a total of 12 bees. In size, ovarian development, and frequency of being mated, the nonqueens were similar to the bees in other nests, all of which lacked individuals that were recognizable as old queens. Therefore, the queen seemed not to be playing a role in inhibiting reproductive development among her nest mates.

III. DISCUSSION AND CONCLUSIONS

With the existing information, there is no way to determine how much of the observed geographical variation in reproductive and nesting behavior is due to the direct effect of environmental differences among regions and how much to genetic differences among populations. Probably, both are involved. The duration of annual activity, of course, varies widely with the climatic zone, thus: Three and one half months at 47° latitude, five and one half months at about 40° latitude, eleven or twelve months at 27° latitude and eleven months (nine with full activity) at about 10° latitude. The seasonal period of inactivity in cool, temperate regions is related to low winter temperatures. Adult, mated females are the only overwintering form. In Florida and the tropics, the inactive period is brief and appears to be related to the dry season. Such inactivity probably occurs

only in places where or years when there is a marked dry season. Survival occurs by adult females of all sorts and, if the dry season is short, by males and even developing immature stages. In the arid, Southwestern United States, the same is probably true, except that the inactive season may be long, due to protracted aridity and probably also winter. Data are needed regarding this species in the Southwest.

In cool, temperate regions *Halictus ligatus* lives in rather shallow, commonly aggregated nests. In Kansas (39°) and more southern localities, the nests are much deeper and are rarely aggregated.

In Trinidad and Colombia, guarding was rarely observed and there was no evidence of specialized, guarding individuals, as are found in *Lasioglossum zephyrum* (Brothers and Michener, 1974). In the cool, temperate zone, however, guarding is common, often by a large-headed bee, probably frequently the queen. Clearly, various types of individuals may be specialized as guards. However, the queen's large head seems to be especially advantageous for closing the burrow entrance. If the queen is essential for survival of the colony, it is surprising that she would often or even sometimes adopt the high risk activity of guarding, but similar behavior is known among large-headed females of certain other halictine species, in contrast to species whose queens have ordinary-sized heads. Perhaps the good guarding qualities of large heads outweigh the danger of being near the soil surface for long periods.

Little is known about colony-establishment in tropical and warm, temperate regions. In the few known cases, nests were started by lone females. This is apparently the strongly predominant method also at about 40° latitude (Indiana). However, at 42° (New York) 25 and 32 percent of the spring nests in

two different years were inhabited by two or more gynes forming a semisocial colony. At 43° (Ontario), 60 percent of the spring-nests contained such colonies. In such a colony, the largest bee ordinarily becomes the queen, the others become auxiliaries or workers which may survive to forage with the daughters. It seems possible that where the active season is short, auxiliaries are important to start activity rapidly. Also, smaller and perhaps reproductively disadvantaged individuals might have lower fitness in such a climate than in warmer areas and hence might attain greater inclusive fitness by joining other females. The situation parallels that found in *Polistes fuscatus* in which gynes often join to form semisocial colonies in the northern, but not often in the southern part of the range (Heather Dew, personal communication).

In Ontario, males apparently are produced throughout the season when daughter females are produced. Thus, they first appear in late June. Perhaps this is important to provide males to mate with females to replace any overwintered queens that die, thus keeping the colonies developing as rapidly as possible through the short season. Farther south, in New York and Indiana, early-summer offspring are all females and males do not appear until late July. In the tropics and probably in Florida, as in Ontario, males are produced throughout the season when females are produced.

Overwintered queens die in July or August, after only a few months of post-hibernation activity, in the higher latitudes. In colonies whose queens die early, daughters can become replacement queens, but apparently they rarely attain fully queenlike ovarian development. In Trinidad, the bees that establish nests may be similarly short-lived, for only one colony was found to contain a probable foundress. Daughter bees and their descendants, however, regularly become reproductive and

maintain the colony for months and perhaps years. Having higher reproductivity than workers in the north, they perhaps also found colonies.

In cool, temperate regions, daughter (i.e., worker) production is more or less continuous after the first daughters mature in late June (latitude 40°-43°) until overwintering females are produced in late summer. In Indiana and New York the maximum number of adult workers found in a nest at any one time was nine or ten. The mean number of mature females in nests in New York was only 4.3 and 3.4 in different years. In the tropics, colonies become larger. One from Trinidad contained 16 females and one from Colombia an estimated 21. The mean, adult female population (six nests only) was 11.3. The two Floridian colonies studied were relatively large and colonies there may attain sizes similar to tropical ones.

Probably, throughout the range, there is a continuum in size from smallest to largest females, with no bimodality. In cool, temperate regions, females produced in late summer have a large average size, mate, overwinter, and establish colonies in the following year. In Trinidad, such large females are produced throughout the season. They may well be important in establishing colonies, as in the north. If so, colony establishment must be scattered through the year. Not all large bees in Trinidad are queenlike, however. Some are unmated and have relatively slender ovaries.

Large females are reported by Chandler to be produced in unusually large cells with elongate rather than subspherical food-masses. Similar large, elongate food-masses were found in a Floridian nest by G. C. and K. R. Eickwort.

In Litte's New York study, the daughter bees that were mated totaled 5.7 percent in July, 17.3 percent in August. The numbers were small and the difference be-

tween the months, while reasonable in view of the increasing male population in late summer, may not be meaningful, as Litte points out. By contrast, in Trinidad, 58.1 percent of the bees that we found associated with nests and 55.6 percent of the foragers were mated. As only a few bees were suggestive of temperate zone queens in large size and much enlarged ovaries, the above comparison of mating frequencies seems reasonable.

Ovarian development, likewise, is much greater among tropical than New York bees. As shown in Table 4, Litte

TABLE 4. Percentages of bees (excluding nest foundresses) from New York and Trinidad having ovaries of various size classes (A-D).

Ovarian class	AB	C	D	N
New York (Litte)	12.6	23.3	64.2	151
Trinidad (associated with nests) ..	53.1	37.5	9.4	64
Trinidad (foragers)	53.6	45.1	1.3	384

found only 12.6 percent of July and August daughters with ovaries of classes A and B. Probably, these were mostly or all replacement queens rather than workers. By contrast, in Trinidad, about 53 percent had enlarged ovaries. All the bees dissected with an oocyte nearly ready to be laid were foragers. In daughter bees in New York, positive relationships exist among head-width, mating, and wing-wear (longevity?). Similar, although not identical, relationships hold in the Trinidad population. A small sample taken in April in south central Florida shows a high percentage of mated bees with enlarged ovaries there also.

In summary, different populations of *Halictus ligatus* have adopted different social strategies as adaptations to differing environments. In cool, temperate regions, spring-nests are occupied by lone individuals or semisocial colonies (sense of

Michener, 1974) of foundresses. In either case a eusocial colony develops in the summer, the queen sometimes being replaced by one of her daughters. In tropical regions, the same sequence is probably followed although simple eusocial colonies with the queen as the only reproductive were not found and this condition is probably short lived. Many of the daughters become reproductive in the tropics but these daughters are not queenlike in behavior, for they regularly forage. The colony thus becomes more nearly semisocial, its maintenance being dependent on egg-laying daughters, or granddaughters, etc. By themselves, such individuals might also be regarded as communal, but there are also other daughters that are not reproductive and that are workers. Clearly, terms like communal and semisocial, while useful for many bees, fail to describe societies such as those in nests of *Halictus ligatus* in the tropics. Words like queen and worker also become difficult to apply successfully. They are helpful but must be used with caution and explanations.

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