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AN ANALYSIS OF VARIATION IN THE NEST ARCHITECTURE OF *HALICTUS LIGATUS* IN ONTARIO

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SUMMARY

Nest architecture of *Halictus ligatus* was studied at Victoria, southern Ontario; over 130 nests were excavated in 1984. The most important findings are as follows. Nest failure was lower in vegetated areas than in bare ground. Nests with entrances hidden under leaves may suffer less mortality from parasites than those out in the open. Loops around cells are dug in response to moist soil conditions and appear to be an intermediate step towards cavity formation. Brood mortality due to mould seemed to result from cell waterlogging which the excavation of loops may help to prevent. Cells near the surface may suffer from waterlogging after heavy rains. Nests situated in denser vegetation suffered less mortality from mould. Gyne-producing cells are larger than male or worker-producing ones. Mandibular wear is an accurate measure of the amount of excavation performed by an individual female.

RESUME

Analyse de la variation de l'architecture du nid chez Halictus ligatus dans l'Ontario

On étudie, dans le sud de l'Ontario, l'architecture des nids de *Halictus ligatus;* on déterre pour cela, en 1984, plus de 130 nids. Les principales découvertes sont les suivantes. La survie des nids est plus grande sur des surfaces recouvertes de végétation que sur des sols dénudés. Les nids dont les entrées sont dissimulées sous des feuilles souffrent moins de mortalité par prédateurs et parasites que ceux dont les entrées sont apparentes. Des boucles entourant les cellules sont construites pour prévenir une trop grande humidité du sol et semblent constituer une étape intermédiaire vers la formation d'une cavité. La mortalité du couvain due à l'humidité semble résulter d'un excès d'eau que l'excavation de boucles pourrait contribuer à prévenir. Les cellules situées près de la surface peuvent souffrir d'un excès d'humidité après de fortes pluies. Les nids situés sous une végétation plus dense souffrent moins de mortalité par moisissure. Les cellules produisant des reines sont plus grandes que celles qui donnent des mâles et des ouvrières. L'usure mandibulaire est une mesure précise du creusement accompli par un individu femelle.

INTRODUCTION

The nest architecture of sweat bees has been the subject of many studies, from the large compilation by SAKAGAMI and MICHENER (1962) which surveyed all of the information available at that time, to numerous brief accounts of individual nests. Although of interest in themselves, nest architectural studies have been used to support both taxonomic and social evolution arguments. However, despite the excavation of many thousands of nests of a wide range of species, there has been very little analysis of the factors that affect intraspecific variation in nest structure. The study described here is an attempt to show, in detail, how aspects of *Halictus ligatus* nest architecture vary between individuals and through the various stages of colony development in a north temperate climate.

METHODS

A large aggregation of *H. ligatus* was discovered by the side of Highway 10, just north of Victoria, Ontario, 43.50° N, 80.00° W, in 1979 by the junior author. The social organisation of this species at this locality was investigated in some detail in 1983 and 1984 and some 200 nests were excavated the majority (130) in 1984, therefore all analyses will use data from this year only unless otherwise stated.

The nest aggregation was at the top of a bank cut into a gently undulating hillside to make way for the highway. The slope faces south west, is at an angle of 40° from the horizontal and is some 15 metres in height. The soil is of clay with sand admixture in some places. The aggregation was densest at or near the top of the slope at the north end, but nests were found all along the length of the bank and as close as 3 metres from the level hard shoulder of the road.

Detailed field observations were made in two areas. Area A was near the north-west extreme of the bank and consisted of a slope, well covered with vegetation, composed largely of various grasses. Nests in this area were shaded by trees until between 9 and 10.30 am. Area C was on flat ground at the top of the bank, the vegetation cover was sparser, consisting mainly of weeds and was not shaded. Less detailed observations were made in area B which was intermediate in slope, ground cover and degree of shading between the other two areas.

Several other halictine species nested at this locality, *Augochlorella striata, Lasioglossum (Lasioglossum) leucozonium* and *L. (Dialictus) heterognathum* were quite common; *L. (D.) zephyrum* and *Halictus (Seladonia) confusus* being present in smaller numbers. Nests of the former three species in particular were often intermingled with those of *H. ligatus*. The predatory sphecid *Philanthus gibbosus* was common, particularly in 1984, and preyed upon all of the aforementioned halictines.

Nests were located by observing bees entering or leaving the burrows during both spring and summer provisioning phases. The positions of all nests in areas A and C were mapped to the nearest cm using a grid quadrat *(fig. 1)*. Vegetation density was estimated by counting the number of quadrat points that touched vegetation with a point density of 400 per square metre. This facilitated the analysis of nest clumping and distribution in relation to ground cover. Many nest entrances were situated directly underneath a leaf of a basal rosette of *Daucus, Taraxacum* or *Hieracium*, the presence or absence of this condition was noted. Most of the plants at site C were species that have a basal rosette of leaves and later develop a central flowering spike. Thus, vegetation cover at ground level did not alter drastically as the season progressed. Site A had a lot of grass in addition to some of the above plants, the vegetation cover here also did not change greatly during the season.

Nest excavation techniques were as described in PACKER and KNERER (1986) except that Johnsons baby powder, and not paprika, was blown down the nest entrances to facilitate successful excavation. Nest entrance and burrow diameters were measured using an eye-piece micrometer, accurate to .1 mm. The depth of various features of the nest, such as the first and last active cells, placement of branch burrows, and greatest depth of the nest etc. were measured using a ruler and total burrow lengths were estimated from the drawings and measurements. Cell lengths and depths were measured, to the nearest 0.5 mm, using a ruler and cell volume was estimated from the formula for the volume of a cylinder

$$V = \pi L R^2$$

where L and R are the greatest length and half of the depth of the cell respectively.

Pollen ball size was measured both by volume and weight. Length, breadth and height were measured to the nearest .5 mm and volume estimated by multiplying the three measurements together. The pollen balls were weighed on an electric balance in the laboratory after having been transported in glass tubes kept in a cooler at around freezing to reduce weighing error due to evaporation. Pollen balls were placed into sex and caste categories as follows. Gyne-producing pollen balls were easily distinguished from male-producing ones by their shape. They were elongate with the ventral surface curved such that only the two ends of the mass were in contact with the floor of the cell, the dorsal surface contained a central, shallow depression which received the egg. Male-producing pollen balls were slightly flattened spheres with only the centre of the ventral surface touching the cell floor. Worker-producing pollen masses were similar in size and shape to male-producing ones but separation of the two was easily done by virtue of the different time of year that they are produced. Almost all pollen balls were assigned to sex and caste in this manner. Only 7 out of 169 could not be classified on the basis of shape alone. It is possible that some errors were made in this categorisation : first (worker) brood male-producing pollen balls could not be distinguished from worker-producing ones and some small reproductive generation females were probably produced from fertilised eggs laid upon male-sized pollen balls (unusually small, overwintered females do occur at low frequencies in this population). However, males made up only 15 % of the first brood (based upon pupal counts). Pollen balls assigned to male and gyne-producing categories did not overlap in weight, but the largest male-producing masses were almost as large as the smallest gyne ones.

Bees loosen soil with their mandibles during excavation and the degree of mandibular wear should indicate the amount of digging performed. The mandibular wear of each nest bee was estimated on a scale from one to five (in a manner similar to that of ORDWAY (1966)). The size of cells and the diameters of the burrows and nest entrances should be influenced by the size of the bees that constructed them. Thus the head widths of all active female bees in the nests were measured.

Rarely was it possible to measure all of the aforementioned variables in any one nest ; for this reason the sample sizes vary greatly between different analyses.

RESULTS AND DISCUSSION

Nest initiation

H. ligatus nests at Victoria, Ontario, were initiated in three ways. Firstly, they were excavated from the surface by gynes that had left their natal nests after overwintering therein ; most nests at this site were initiated in this

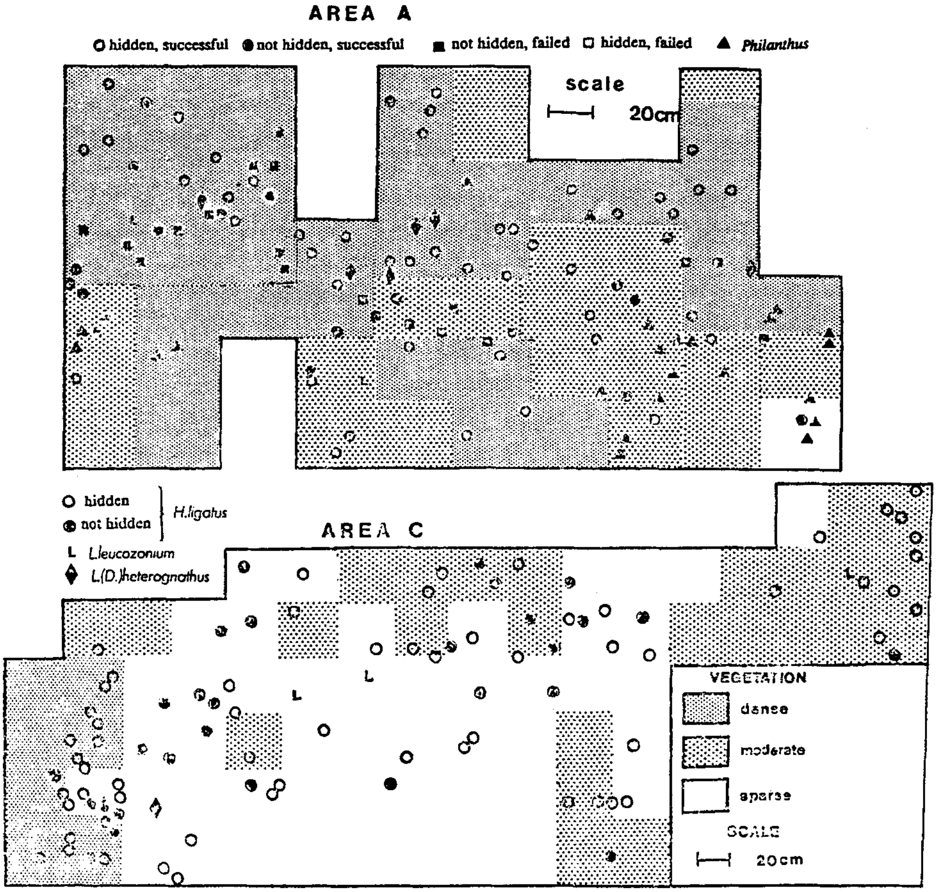

Fig. 1. — Maps showing distribution of nests at study sites A and C. Limits to the distribution of the different vegetation densities are approximate. Note that the scales are different for the two areas.

Fig. 1. — Carte de distribution des nids dans les sites A et C. Les limites de distribution des diverses densités de végétation sont approximatives. Noter que les échelles sont différentes dans les deux sites.

manner. Secondly, females could burrow upwards from their hibernacula, or nearby natal burrow, in early spring and use the emergence tunnel so dug as a basis for their nest. At least one clear instance of this was established in 1983 : two adjacent nests were found to connect at a much greater depth than that reached by any other nests excavated at the same time of year. Partial remains of the previous year's nest were found between these two nests. The clumping together of two or more nests at unusually short distances as shown in *figure 1* is probably a result of nest initiation in this manner. This means of nest initiation has been reported before only in *Lasioglossum (Evylaeus) duplex* by SAKAGAMI and FUKUDA (1972). Thirdly, one or more gynes may reuse their natal nest or a part of it. It is likely that many of the polygynous associations arise when two or more gynes have overwintered in the same nest and remain together as a unit in spring (KNERER, 1980).

L. leucozonium generally started nesting later in the season than *H. ligatus* and began pollen foraging at least one week later. Females of this solitary species were observed on several occasions attempting to usurp nests of *H. ligatus.* At least one attempt was partially successful, in that the *L. leucozonium* female temporarily occupied a *H. ligatus* nest which reverted to its original owner after a few days. *L. leucozonium* females nested in areas of bare soil and thus only *H. ligatus* foundresses that had initiated nests away from vegetation cover were subject to usurpation attempts.

Nest emplacement

Eighty-one nests of *H. ligatus* were mapped in area A and 92 in area C, at a time when worker activity was at its peak. *Figure 1* shows the distribution of nests in relation to the degree of ground cover and also shows whether the nest entrances were hidden by vegetation. In area A, 52 out of 81 nest entrances were hidden by vegetation. 1074 quadrat points fell on vegetated ground out of a total of 1872 samples. Thus, nest entrances were not situated under leaves more often than could be expected by chance ($\chi^2 = 1.53$, $p > 0.05$). However, area C was more sparsely vegetated with only 752 out of 2772 quadrat points falling on covered ground. 60 out of 97 nest entrances were situated under vegetation cover. This indicates that more nest entrances occurred under vegetation cover than are expected by chance ($\chi^2 = 25.2$, $p < 0.0001$). The difference in choice of nest site in the two areas could result from the different types of vegetation encountered : area A being mostly grass covered whereas weeds formed the vegetation in area C. It is likely that nest initiation under a basal rosette of a composite or umbellifer is easier to achieve when the surrounding grass cover is sparse. Nest site choice may be made after careful searching by the foundress but, presumably, it is possible for bees digging their way up from below to locate the position of suitable cover by following the paths of plant roots.

Area B was censused at the peak of foundress provisioning in June. This area was broken into four portions, two had earth placed upon them late in the summer of 1983, the remainder were unaltered. Bees could initiale nests in bare soil or in ground that had a good growth of grass and vegetation as in area A. The census was repeated three weeks later so that the proportion of surviving nests in areas with different cover could be calculated. Defunct nests were easily identified because the entrances had been widened into large holes by rain; entrances of active nests were well maintained and narrow or had small plugs of excavated soil in them. Out of 17 nests initiated in bare soil, only 3 had survived whereas for nests with hidden entrances 14 out of 24 were still active. This difference is highly significant ($\chi^2 = 17.0$, $p < 0.001$) indicating the advantage to be gained in nesting in a substrate with at least some vegetation cover. It is not known whether gyne mortality or nest abandonment caused this result. However, the initial census took place after most females had been provisioning for some time, thus some investment in addition to mere nest excavation had been made before the gyne died or abandoned the nest.

Nests in area A were mapped in late July, when workers were active. This area had been observed in detail during the spring provisioning phase and 81 nests had been marked. Of these, 52 had entrances hidden by vegetation. 47 (90 %) of these nests were still active in late July whereas of the 29 nests with unhidden entrances only 19 (65 %) had survived. This difference is significant (Fisher's exact test, $p < 0.01$).

Bombyliids, rhipiphorids and miltogrammine parasites were found in some excavated nests in area C and their presence or absence was tested against the emplacement of the nest entrance. Sample sizes for the effect of miltogrammines and rhipiphorids were very small but only when their effect was added to that of the bombyliids was any significant association between the presence of parasitism and the location of the nest entrance statistically significant. Each of the nine nests without vegetation over the entrance contained one or more parasitised cells, whereas 12 of the 20 with a hidden entrance had suffered some mortality (Fisher's exact test, $p = 0.029$). However, when the frequency of parasitised cells, instead of parasitised nests, was analysed, even this difference disappeared. Twenty-one of 113 cells (18.6 %) in nests without hidden entrances were parasitised, whereas the figures for nests with hidden entrances show that 47 of 177 cells (26.5 %) were parasitised ($\chi^2 = 2.43$, $p > 0.05$). Larger sample sizes would probably have shown a significant association between parasitism by bombyliids and the nature of the nest entrance. These flies use visual cues to locate host nests as was shown by their interest in holes poked in the soil with a pencil. They oviposit whilst hovering over the nest entrance and flick their eggs down the burrows. This must be more difficult when the nest entrances are hidden. However, returning pollen laden foragers often take longer to locate their own nest entrance and this gives miltogrammine flies in particular help in finding a host nest. Ants and conopids may also strike at this time.

A major mortality factor in bee nests often results from the activities of other, cleptoparasitic, bee species. *Sphecodes dichrous* has been suggested as being a cleptoparasite of *H. ligatus* (KNERER, 1980), and this halictine bee was observed not uncommonly around the nest site. However, not one of the hundreds of nests that were excavated during the course of this study contained a pupa or adult of this species. It therefore seems probable that some other host is utilised by this brood parasite.

In area A there was a nest survival rate of 77 % (41 of 52) from the spring activity phase until the emergence of workers in summer. Litte found a similarly high survivorship (75 %) in nests at this phase of colony development in New York. The reason for the mortality or abandonment of the defunct nests is not known. The causes of nest failure even in area C, which was observed intensively throughout the flight season, were rarely known. It is likely that ant predation played a role and earthworms destroyed several burrows in each year. Foundress mortality during provisioning is also probable but this would not explain the differences in survivorship between nests in bare ground and those near vegetation and between nests with hidden and obvious entrances. Nest abandonment may have caused this result.

Nearest neighbour analyses on nest dispersion in areas A and C indicated that there was no significant difference from the null hypothesis of random emplacement, when the areas as a whole were considered or when only patches of similar vegetation density were included. For area C, the expected mean inter-nest distance was 11.9 cm, for area A this figure was 14.3 cm whereas the observed distances were 13.6 and 15.7 cm respectively. However, there were more nests in the more highly vegetated portions of both areas A and C. When the degree of vegetation cover was divided into three groups (0-9, 10-19, and 20 or more quadrat points in touch with the vegetation) there were significantly more nests than expected amongst the densest vegetation in area C ($\chi^2 = 14.6$, $p < 0.0001$). In area A the difference bordered on significance ($\chi^2 = 3.77$, $p > 0.05$). This could result from foundress nest site choice. Additionally, the improved survival of nests in vegetated areas in the previous year could have had an effect through those foundresses that reused their natal nest in spring or initiated nests in close proximity to their natal burrow.

The presence of dense vegetation cover may alter the edaphic conditions of the soil underneath. It is interesting to note that significantly more nests that were situated in sparsely vegetated ground (less than 10 out of 36 quadrat points falling on vegetation) contained one or more mouldy cell(s) ($\chi^2 = 4.01$, $p < 0.05$). This may be due to the protection from waterlogging given to the nests situated under vegetation or from the drying effect of water uptake by the root system.

Nest structure

The nest architecture of *H. ligatus* has been described by many authors (Chandler, 1955 ; Sakagami and Michener, 1962 ; Kirkton, 1968 ; Roberts, 1972 ; Michener and Bennett, 1977 ; Knerer, 1980 ; and Eickwort, 1985). In only two respects did the nest architecture of *H. ligatus* at Victoria differ from that described for other north temperate populations of this species by Michener and Bennett.

Firstly, there was a high frequency of horizontal or near horizontal portions to the branches from the main burrow. These shallowly angled portions bore comparatively fewer cells than the more vertical parts.

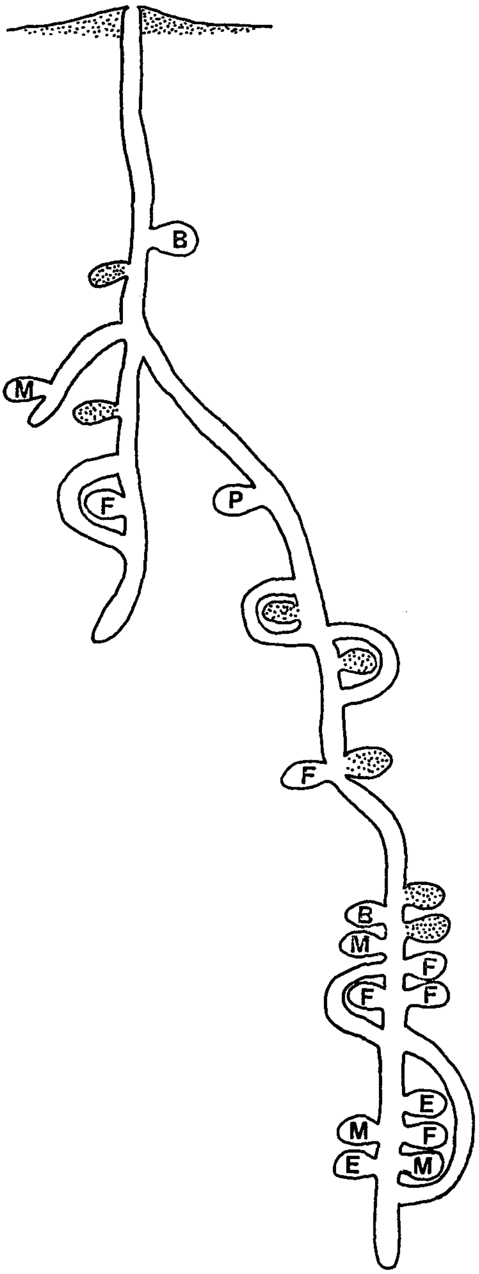

Fig. 2. — Diagram of a nest of *Halictus ligatus* excavated in late August 1984 illustrating the unusual loops in the burrows of some nests in this population. The symbols inside the cells are as follows : B = Bombyliid larva, F = female pupa of *H. ligatus*, M = male pupa of the same, E = empty and P = pollen ball.

Fig. 2. — Diagramme d'un nid de *Halictus ligatus* déterré à la fin d'août 1984 illustrant les curieuses boucles présentes dans les conduits de quelques nids de cette population. Symboles inscrits dans les cellules : B = larve de Bombyliide, F = nymphe femelle de *H. ligatus*, M = nymphe mâle de *H. ligatus*, E = vide, P = pain d'abeille.

The main difference between these nests and those previously described was the presence of looped branches. Towards the end of the spring provisioning phase, several nests were found to contain short branches that bore no cells. Some of these curved back to rejoin the burrow further up, thus making a loop whereas in others the reconnection was not made. In most cases these loops and " incomplete loops " surrounded one or more active brood cells. More loops and incomplete loops were found in many summer nests, particularly at the end of the summer provisioning phase *(fig. 2)*. As in the spring phase, these almost always surrounded active cells with brood. Two hypotheses were put forward to explain the presence of these structures.

1) They were excavated in response to the presence of bombyliid larvae that preyed upon the brood. It seemed that bombyliid larvae often require two prepupae or young pupae to complete their development. Evidence for this is as follows. Fully grown bombyliid larvae are larger than male *H. ligatus* pupae or prepupae, large parasite larvae were often found on a host that was comparatively healthy and had not been largely consumed and a parasite was often found in a cell which was adjacent to an empty cell with a narrow burrow joining the two cells. Thus, these dipterous larvae probably burrow through the soil in order to get from one cell to another. If cells in parasitised nests had a partial cavity around them then it is possible that the adult bees could intercept and perhaps kill these larvae.

There was a significant association between the presence of parasites and loops in the nests. However, both bombyliid larvae and the extra excavations appear more towards the end of the spring and summer provisioning phases and both could be due to other, time related factors. For this reason, the data for excavations between July 23rd and August 1st and August 2nd and August 12th were analysed separately to control for the confounding factor of nest age. No significant association between extra excavations and the presence of bombyliid larvae was found.

2) The presence of complete and partial loops could be a response to overly damp soil, increasing the rate at which the earth around the cells would dry out.

Dead, mouldy cell contents appeared to occur more frequently in nests excavated soon after a heavy rainstorm ; as noted by CHANDLER (1955), mouldy cell contents were often pushed to the back of the cell by the addition of soil. Thus, the extra excavations may improve brood survivorship by increasing soil drainage around the cells.

One hundred and sixty six cells were present in nests that contained one or more loops. Thirty nine of these cells were actually surrounded by loops. Two of these 39 cells (5.2 %) had mouldy or diseased contents whereas 20 of the remaining 127 cells (15.7 %) had died of these causes. The difference in frequency of deceased cell contents between " looped " and normal cells is almost significant (Fisher's exact test, $p = 0.067$).

Eighty-four percent of these loops surrounded one or more brood cells. In cases where cells were not found, it is possible that earth filled old cells were not noticed during excavation. Cells which were surrounded by a loop contained brood of a wide variety of ages. It seems probable that the loops were constructed after the cell(s) had been provisioned in order to prevent cell contents from becoming mouldy after rain.

The plesiomorphic state for halictid nest architecture is a single burrow with the cells at the end of short branch burrows. This condition is found in many of the Halictini, but not in the Augochlorini (EICKWORT and SAKAGAMI, 1979). Derived states include I) the reduction of the cell bearing branch until the cells arise more or less directly from the burrow, II) the clustering together of cells, III) excavation of a cavity around the cell cluster or IV) the excavation of a cavity and the construction of a cell cluster within the cavity. All bees of the genus *Halictus* share a common nest architecture with sessile cells arising from the burrow without any cavity formation with the sole exception of *H. quadricinctus*, a cavity builder (KNERER, 1980). The presence of loops and incomplete loops around brood cells in the nests of *H. ligatus* described above may represent an intermediate stage towards cavity construction. Clearly, however, the excavation of loops around groups of one or more cells is inefficient in comparison to the neat cavities around the cell clusters of all true cavity excavating halictines.

It has been argued that the presence of a cavity is an adaptation to nesting in soils of high humidity by increasing the rate of soil moisture evaporation immediately around the brood cells (PACKER and KNERER, 1985). The observation that the extra excavations carried out by *H. ligatus* females at Victoria seemed related to periods of recent heavy rainfall supports the idea that they are a step towards cavity construction and that cavities may prevent mortality due to soil waterlogging.

Of the other halictine species discovered nesting at this site, only *Augochlorella striata* constructs a cluster of brood cells surrounded by a cavity. The nests, and therefore the brood cells, of this species occurred at shallow depths in comparison to those of the other halictines. It is probable that waterlogging of brood cells after a heavy rain is more likely in shallow nests thus necessitating cavity construction. However, it is difficult to distinguish between phylogenetic-historical and adaptationist explanations in this instance.

CHANDLER (1955) is the only author to have described shallow, horizontal lateral branches ending in an expanded cavity in *H. ligatus* nests. This feature was not found in any of the nests at Victoria.

Nest dimensions

Nest entrances were circular with a mean diameter of 3.32 mm (S.D. = 0.63, N = 37). The mean burrow diameter was 5.66 mm (S.D. = 0.44, N = 49), almost twice the size of the entrance. Entrance diameters showed no relation to queen head width even during the provisioning phase in monogynous nests when the queen was the only bee present ($b = -0.013$, $p > 0.05$, $N = 11$). However, the burrow diameters correlated well with the queen head width both before and after the emergence of the worker brood with queen head width explaining 63.4 and 39.6 % of the variation in burrow diameter in nests before and after the emergence of workers respectively (the regression equations being $y = 0.99x + 2.99$ and $y = 0.82x + 1.69$).

There was no significant difference in burrow diameter before and after worker emergence (mean diameter before worker emergence = 5.75 mm, S.D. = 0.43, $N = 13$; after worker emergence = 5.66, S.D. = 0.43, $N = 33$, $t = 0.61$, $p > 0.5$). But nest entrance diameters were significantly smaller after the emergence of the worker brood (before diameter = 3.65, S.D. = 0.89, $N = 11$, after = 3.17, S.D. = 0.43, $N = 26$, $t = 2.22$, $p < 0.05$). This indicates that workers narrow the nest entrance, presumably to make nest guarding more effective, but do not alter the diameter of the nest burrows. It is worth noting that none of the nest entrances were narrower than the head width of the queens within them; a situation which has been reported for *Lasioglossum* (*Evylaeus*) *malachurum* (KNERER, 1973) and *Halictus (Seladonia) hesperus* (PACKER, 1985) — species with a much larger morphological caste difference.

Figure 3 shows the change in greatest nest depth throughout the colony cycle. There is a general increase in depth as the season progresses, the significance of this pattern being demonstrated with Spearmans rank correlation ($r = 0.62$, $p < 0.0001$, $N = 64$).

The mean greatest nest depth before worker emergence was 11.3 cm (S.D. = 1,9, min. = 8, max = 15, $N = 24$). After worker emergence, the nests averaged 16.3 cm in depth (S.D. = 3.0, min. = 11 max = 23, $N = 35$). The difference in depth is significant ($t = 7.3$, $p < 0.0001$). Nests at Victoria are, therefore, a little shallower than those in New York which averaged 15 cm deep during the spring phase and 18 cm in summer (LITTE, 1977).

Brood cells ranged from 5 to 13 cm in depth in spring (only extreme depths were recorded so means cannot be calculated) and from 6 to 20 cm in summer. These figures being somewhat shallower than those recorded by KIRKTON in Indiana (7.5 to 12.5 cm in spring and 15 to 30 cm in summer). Active worker brood cells were contemporary with the first reproductive brood cells in 25 nests. Brood of the two generations were mixed along the length of one or more nest branches in 13 of these nests. Despite this high incidence of intermingling of cells from the two broods, the depth of the most recently excavated cell was significantly greater in nests in the summer provisioning phase than in the spring phase (spring recent cell mean depth = 8.5 cm, S.D. = 1.5, $N = 11$; summer mean depth = 12.2, S.D. = 3.1, $N = 30$; $t = 5.1$, $p < 0.0001$). Similarly, the rank correlation of most recently excavated cell depth with age of the nest is also highly significant (Spearmans rank

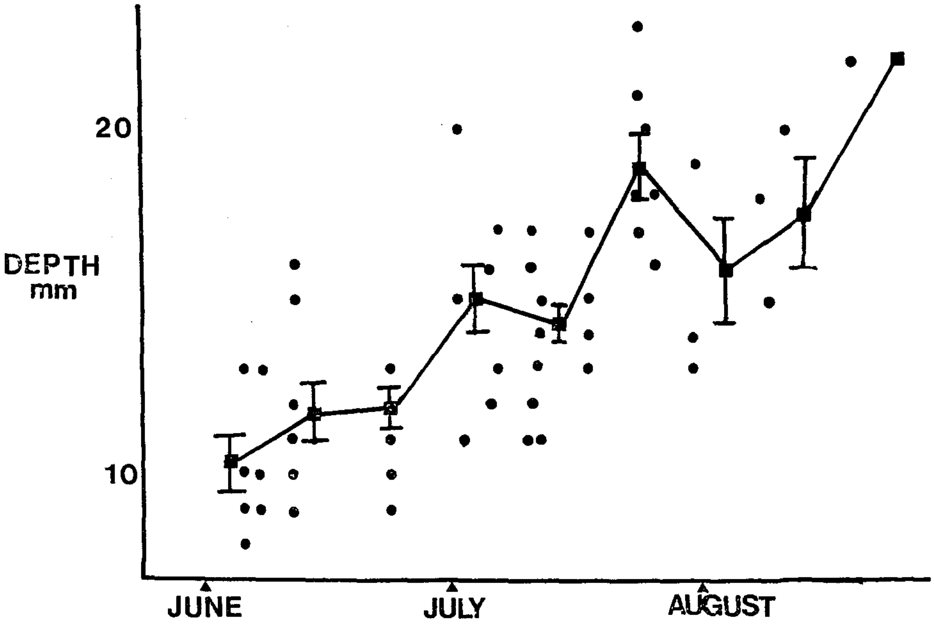

Fig. 3. — Variation in greatest depth of the burrow for *H. ligatus* nests in area C in 1984. Each dot represents one nest depth and each square represents the mean, plus standard deviation, of depths for the nests excavated within a 10 day period. The small triangles along the horizontal axis indicate the 15th of each month.

Fig. 3. — Variation de profondeur du conduit dans les nids de *H. ligatus* du site C en 1984. Chaque point représente la profondeur d'un nid et chaque carré la moyenne, plus la déviation standard, des profondeurs des nids déterrés pendant une période de 10 jours. Les petits triangles le long de l'axe horizontal indiquent le 15 de chaque mois.

correlation coefficient = 0.54, $p < 0.0001$, N = 18). Thus the most recently excavated cells occur at deeper levels as the season progresses *(fig. 4)*. This is a general phenomenon in halictine nesting biology (Sakagami and Michener, 1962) and two reasons have been suggested for it. Firstly, the dry soil nearer the surface may be too difficult for the bees to work with. Secondly, there may be a lower limit to the moisture content of the soil that a developing larva can tolerate. May (1970, 1972) has shown that the larvae of *Augochlora pura* absorb a large amount of water during their development, amounting to 62 % of their final body weight. Clearly this would not be possible if the soil were too dry.

Sixty cells excavated in 1984 had mouldy contents, in all cases the pollen balls or larvae were comparatively wet. In relation to the remaining, healthy, active cells in the same nests 27 of the mouldy cells were at a deeper level than the median cell depth and 27 were shallower. Mouldy cells seemed

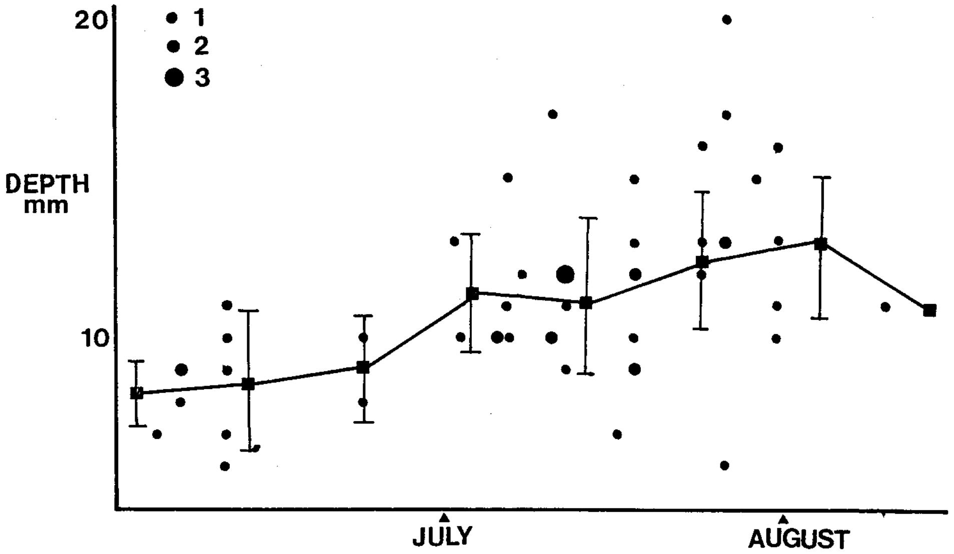

Fig. 4. — Variation in depth of the most recently excavated cell for *H. ligatus* nests in area C, 1984. Each dot represents one to three cell depths. Rest of legend as in *fig. 3*.

Fig. 4. — Variation de profondeur de la cellule la plus récemment creusée dans les nids de *H. ligatus* du site C, en 1984. Chaque point représente les profondeurs de 1 à 3 cellules. Reste de la légende : voir *fig. 3*.

to occur more frequently after a rainy spell. This possibility was tested as follows. The proportion of cells that had mouldy contents was calculated for each day that excavations were made. A 2 × 2 contingency table was drawn up comparing the frequency of increases and decreases in the proportion of mouldy cells since the previous excavations and whether or not there had been precipitation in the intervening period. A Fisher's exact test revealed a significant association between recent rainfall and an increased frequency of mouldy cell contents ($p = 0.0059$). Thus, mortality due to mould may result from soil waterlogging. This may place a premium on constructing cells at a depth above the dampest layers of the soil but beneath the depth to which the earth becomes waterlogged after a heavy rainfall.

The number of branches, the total depth and length of the burrow and the number of active cells correlate significantly with the number of workers in summer nests (Spearmans rank correlation coefficient = 0.33, $p = 0.01$, $N = 59$ for number of branches ; $r = 0.47$, $p < 0.005$, $N = 40$ for greatest depth ; $r = 0.54$, $p < 0.0005$, $N = 39$ for total length of the burrows and $r = .43$, $p = 0.0005$, $N = 63$ for the number of cells). Because the number of branch burrows varies with the number of active females in the nest, the cells being provisioned may be comparatively widely spaced at any one time.

It is possible that this is a result of interindividual competition for oviposition sites within the nest. Queens of *H. ligatus* have relatively poor powers of ovarian inhibition over their workers (PACKER, in prep.). It could be difficult for a queen to oviposit and ensure the continued survival (prevent oophagy) of her eggs in several widely spaced cells at the same time.

Cell size

Mean cell volumes for worker, male and gyne-producing pollen balls were respectively 1.16 cm^3 (S.D. = .08, N = 5) ; 1.04 cm^3 (S.D. = .21, N = 13) and 1.45 cm^3 (S.D. = .21, N = 23). Analysis of variance with Scheffe's *a posteriori* test of significance revealed that gyne-producing cells were significantly larger than male-producing cells at the .01 level and larger than the worker producing cells at the .05 level of significance.

There are significant relationships between cell volume and both pollen ball volume and pollen ball weight ($b = 0.46$, $p < 0.005$ and $b = 0.47$, $p < 0.01$ respectively). However, there were no significant correlations between cell volume and queen head width for cells containing worker, male or gyne-producing pollen balls. Neither was there any significant relationship between the mean size of workers and the volume of male or gyne-producing cells. However, there was a significant positive correlation between the number of workers and the volume of male-producing cells ($r = 0.77$, $p < 0.005$, $N = 13$).

The finding that gyne-producing cells are significantly larger than both worker and male-producing ones is of some interest because it indicates that the decision to produce a male or female reproductive may, in part, precede the provisioning of a cell — occurring at the time of cell excavation. The significant relationship between cell volume and pollen ball volume and weight indicates that cells may receive different amounts of pollen according to their size. This means that events occurring perhaps as much as several days prior to oviposition may play a role in the determination of the sex of the egg laid. It is interesting to note that artificial addition of pollen to the provision masses in cells of *Lasioglossum (Evylaeus) calceatum* results in an augmented proportion of females in the first brood of this very primitively social species (PLATEAUX-QUÉNU, 1983). Worker and reproductive brood cell sizes differ in this species, but it is not known whether male and female-producing cells differ in dimensions (PLATEAUX-QUÉNU, 1973).

KAMM (1974) and KUMAR (1975) have investigated the factors that affect cell size in *Lasioglossum (Dialictus) zephyrum* under controlled laboratory conditions. They found that cell size and the size of the bee that emerged from it were positively correlated. Cell size increased with decreasing day length and temperature and with an increase in the number of adult bees in the nest at the time the cell was built and provisioned. Cell size also correlated positively with the size of the individual that constructed it and with the mean size of the bees in the nest. In contrast, we did not find a significant positive relationship between queen head width and the size of the cells that she constructed.

Mandibular wear

Because nest excavation takes place via the action of the mandibles, a correlation between mandibular wear and nest size is to be expected. In nests prior to the emergence of the first workers, queen mandibular wear correlated well with the total burrow length but not with the number of cells (Spearmans rank correlation coefficients are 0.58, $p < 0.05$, $N = 16$ and — 0.15, $p = 0.5$, $N = 22$ respectively). After worker emergence, the mandibular wear of all of the adult females in the nest correlates well with both the number of active cells and total burrow length (Spearmans rank correlation coefficient $= 0.39$, $p < 0.005$, $N = 61$ and 0.51, $p < 0.005$, $N = 37$ respectively). This relationship is due to excavation performed by workers as is shown by comparing the results obtained separately from correlations of queen and worker mandibular wear with burrow length and number of cells. Thus, for queen mandibular wear the relationships are : Spearmans rank correlation coefficient $= 0.13$, $p > 0{,}5$, $N = 43$ and 0.11, $P > 0.5$, $N = 29$ for burrow length and number of cells respectively, whereas for worker mandibular wear the results are $r = 0.38$, $p < 0.05$, $N = 41$ and $r = 0.73$, $p < 0.0001$, $N = 37$. Queens in summer nests with workers do not have significantly more mandibular wear than those in spring nests with a full complement of worker brood cells (Mann-Whitney U test, $U_s = 442$, $t_s = 1.8$, $p > 0.05$). The queen does perform some excavation after the emergence of the workers but presumably only a small proportion of the total.

Mandibular wear, in association with the degree of wing wear, is often used as an indicator of relative age in studies of halictine bees. However, variation in these characteristics really represents the amount of excavation work and the amount of foraging performed respectively and thus, " lazy " bees may appear to be younger than they really are. This study establishes a clear relationship between mandibular wear and the amount of nest excavation.

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