

Nest architecture and brood mortality in four species of sweat bee (Hymenoptera; Halictidae) from Cape Breton Island¹

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The nest architecture of four species of the bee family Halictidae from Cape Breton Island, Nova Scotia, was studied. *Augochlorella striata* and *Lasioglossum (Evylaeus) comagenense* constructed their brood cells in a cluster surrounded by a cavity. In the case of *A. striata*, the cavity-forming habit increased the rate at which the soil of the brood cell cluster dried out, relative to the surrounding soil. The year of the study was unusually dry and in midsummer the moisture content of the soil was extremely low. This weather pattern seemed to result in some mortality of *A. striata* brood due to dehydration, and prevented foundresses from constructing brood cells. The two other species, *Lasioglossum (Evylaeus) cinctipes* and *Lasioglossum (Dialictus) laevissimum*, did not construct brood cell clusters. All four species had shallower nests than other species with similar nest architectures for which published data are available. All species except *L. laevissimum* nested in association with stones at the ground surface. It was shown that brood cells of nests situated close to rocks and stones were likely to experience increased temperature, presumably resulting in a faster developmental rate for immatures. This may be important in the Cape Breton environment, which is clearly marginal for social sweat bees. Both *A. striata* and *L. comagenense* exhibited very low mortality rates in developing immatures (1 and 7%, respectively).

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On trouvera ici des données sur l'architecture des nids de quatre espèces d'Halictidae de l'Île du Cap-Breton, Nouvelle-Écosse. Chez *Augochlorella striata* et *Lasioglossum (Evylaeus) comagenense*, les cellules larvaires sont rassemblées en groupes et entourées d'une cavité. Dans le cas d'*A. striata*, la formation de la cavité entraîne la déshydratation plus rapide de la terre qui forme les cellules que du sol environnant. L'année de l'étude s'est avérée une année particulièrement sèche et, au milieu de l'été, le contenu hydrique du sol était extrêmement bas. Ces conditions semblent avoir entraîné une certaine mortalité par déshydratation au sein du nid des *A. striata* et elles ont empêché les fondatrices de construire de nouvelles cellules larvaires. Les abeilles des deux autres espèces, *Lasioglossum (Evylaeus) cinctipes* et *Lasioglossum (Dialictus) laevissimum*, n'ont pas construit de cellules regroupées. Les quatre espèces avaient des nids peu profonds par comparaison aux données de la littérature sur d'autres espèces à nids d'architecture semblable. Chez toutes les espèces, sauf chez *L. laevissimum*, les nids étaient associés à des pierres à la surface du sol. Il a été démontré que les cellules larvaires des nids situés près de pierres ou de cailloux sont plus susceptibles d'avoir des températures plus élevées et favorisent donc le taux de développement des larves. Ce facteur a probablement une grande importance dans un environnement comme celui de l'Île du Cap-Breton qui constitue un milieu plutôt marginal pour des Halictidae sociaux. Les taux de mortalité enregistrés chez *A. striata* (1%) et chez *L. comagenense* (7%) étaient très faibles.

[Traduit par la revue]

Introduction

Members of the bee family Halictidae (the sweat bees) exhibit a wide variety of nest architectures. Since the early compilation of data by Sakagami and Michener (1962), the nests of additional species have been described, measured, or figured. However, little has been achieved in terms of understanding the functional significance of the great variation in architecture observed within the group or of the factors that determine nest density and location.

Comparative studies of variation in nest characteristics within and between species may provide some insights into the selective forces that have guided the evolution of sweat bee nest architecture. The present paper describes variation in nest architecture of four sympatric species found on Cape Breton Island, Nova Scotia: *Augochlorella striata*, a member of the tribe Augochlorini, and three species of the tribe Halictini,

Lasioglossum (Evylaeus) comagenense, *Lasioglossum (Evylaeus) cinctipes*, and *Lasioglossum (Dialictus) laevissimum*. The social organization and phenologies of these species are described elsewhere (Packer et al. 1989). Ordway (1966) provided detailed descriptions of nest architecture and construction for some Kansas populations of *A. striata*.

Because a large proportion of the mortality observed in the most intensively studied species (*A. striata*) appeared to result from microclimatic effects, data on brood mortality are also presented.

Methods

The study areas

Fieldwork was carried out in the Loch Lomond – Irish Cove area of Cape Breton Island, Nova Scotia, in the autumn of 1986 and throughout the flight season in 1987. Figure 1 shows the precise location of the three study areas. *Augochlorella striata* was studied at Irish Cove (45.48°N, 60.40°W, ~40 m above sea level) on the north and east slopes of a shallow roadside excavation. Gravel extraction had occurred there in 1966–1967. *Augochlorella striata* nests were concentrated on slopes in areas where the grass cover was not thick and where many rocks and stones occurred on the ground surface. *Lasioglossum cinctipes* was studied at the Salem Road Pit (45.47°N, 60.37°W, ~70 m above sea level) at the side of an access road leading to a landfill site. The area had been cleared around 1979–1980.

¹Dedicated to Prof. C. D. Michener on the occasion of his retirement.

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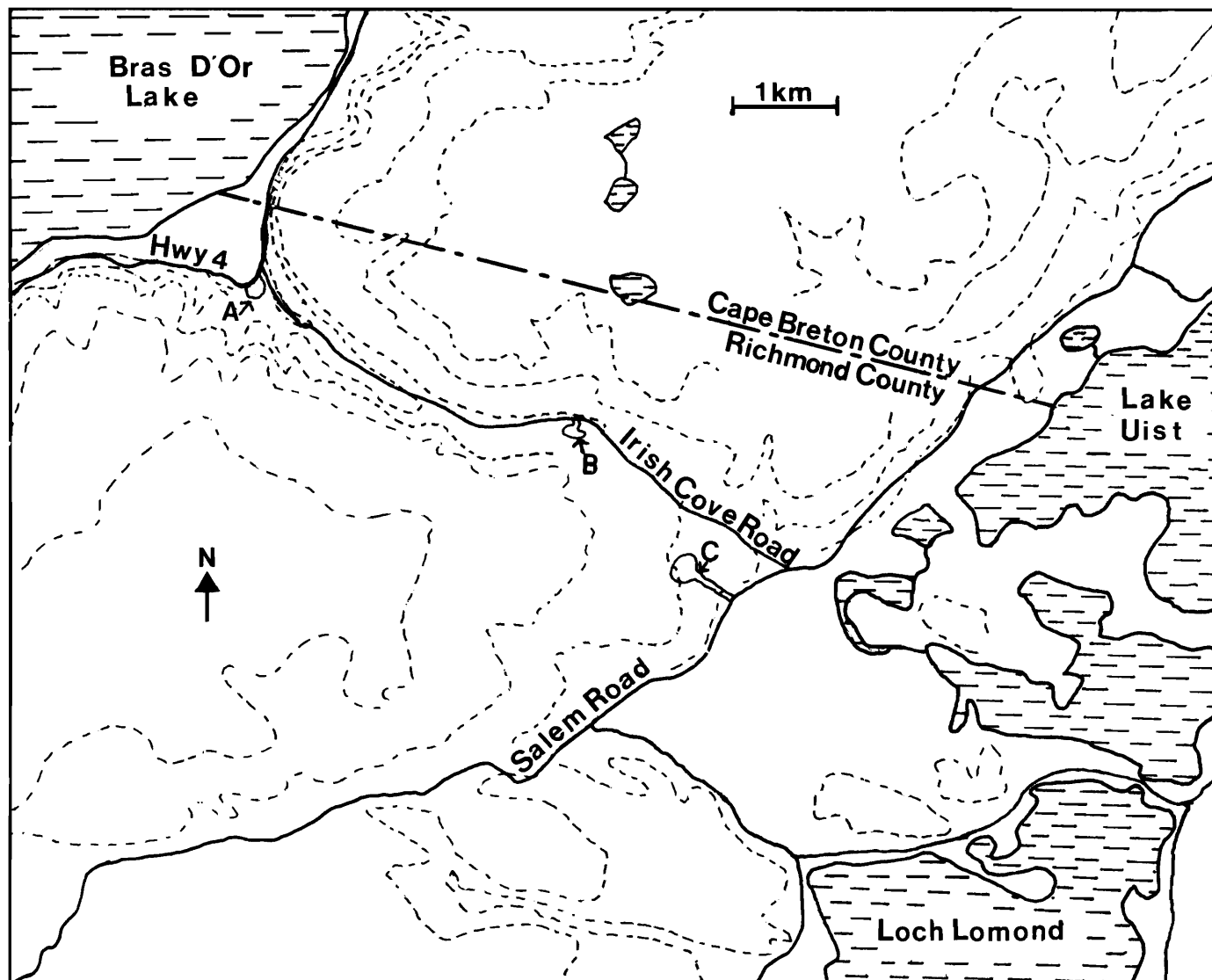


FIG. 1. Map showing location of study sites: A, *A. striata* study site; B, *L. comagenense* study site; C, *L. cinctipes* study site. *Lasioglossum laevisissimum* was studied at site B and along the northeast side of the access road to site C. The entire area is covered with white spruce or mixed hardwood – white spruce woodland, with the exception of a few (mostly abandoned) farms along the Salem Road, some marshy areas, and some roadside cottages along Highway 4. (Based upon Energy, Mines and Resources Canada map 11F/15.)

The bees nested in a small sandy hump, the surface of which was covered with many rocks and stones. A few nests of *L. comagenense* were also found in this area but the main site for this species was the Irish Cove Road Pit (45.47°N, 60.38°W, ~80 m above sea level), another gravel extraction site. Nests were found in two areas: one was flat and sandy, with some rocks and pebbles on the surface; the second was a loose pile of gravel, stones, and sand separated from the first area by a few *Alnus* bushes. *Lasioglossum laevisissimum* was found in all three of the aforementioned sites but data were collected only from the Salem Road and Irish Cove pits. At the former, most nests were in the 1 m high embankment along the side of the access road. At the Irish Cove Road Pit this species nested, along with *L. comagenense*, in the flat sandy area. The nesting biology of *L. laevisissimum* will be described in least detail of the four species: most nests were excavated by Dr. G. Eickwort, who is preparing an article on *L. laevisissimum*.

Field techniques

Nest positions were marked with bamboo skewers with numbered tags on the top. For *A. striata* and *L. cinctipes*, the distance between each nest and its nearest neighbour was measured. Nest dimensions,

such as entrance and burrow diameters, and maximum and minimum cavity depths, were recorded in the field. For *A. striata*, internal cell lengths and depths were recorded using a binocular microscope and eyepiece micrometer.

Soil temperature and moisture

Stones may increase the warmth experienced by developing brood in adjacent nests. This hypothesis was tested on July 20, 1987. Three thermometers were placed with their bulbs 5 cm beneath the soil surface. One was placed in soil free of rocks and stones, the second where small stones and pebbles covered the surface (size ranging from 3 to 5 cm diameter), and the third with the bulb adjacent to a large rock (diameter approximately 15 cm). All three thermometers were within 20 cm of each other and the portions above ground surrounded by tinfoil. Temperatures were recorded almost every half hour between 11:00 and 21:00.

The cavity-constructing habit may reduce the probability of brood cells becoming waterlogged (Packer and Knerer 1985). To test this hypothesis, samples of earth were taken from cell clusters and the soil immediately adjacent to the nest cavity on two separate occasions, July 11 and August 14, 1987. Entire brood clusters and associated

soil samples were wrapped in Saran Wrap®, kept on ice and transported to the laboratory. Brood cell clusters were dissected; pollen balls, bee immatures, and any fecal matter were removed; and the remaining soil was wrapped in tinfoil, weighed, and dried in an oven at 80°C to constant weight. Soil taken from the sides of nest cavities was also weighed, dried, and reweighed. Pieces of gravel were separated from the dried earth and weighed separately and their weight was subtracted before percent weight loss upon drying was calculated. Angular transformations of these data were used in the analyses.

Results

Nest architecture

Augochlorella striata

Augochlorella striata constructs turrets at the nest entrance (Figs. 2a–2c). These turrets are built from soil displaced by the bees during nest excavation. Turrets ranged from 0 to 51 mm in height (Table 1). Turrets were not repaired during dry weather, but on the morning after a heavy rainfall on June 28, all surviving foundresses in one nest cluster ($N = 32$ nests) could be seen repairing their turrets. Dry soil conditions likely preclude turret construction and repair. The nest entrance at the apex of the turret was significantly narrower than the burrow diameter at ground level (ground level diameter = 3.76 mm, SD = 0.56, $N = 63$; $t = 7.48$, $p \ll 0.001$). Burrow diameters beneath the ground surface were significantly wider than at ground level (Table 1; $t = 6.99$, $p \ll 0.001$). A blind-ended burrow beneath the soil surface was found in 13 of 44 (29.5%) nests for which detailed data were collected during the first foraging period. After daughter emergence almost all nests had a blind burrow beneath the cell cluster and by August no nests containing adult females were without one. The deeper overwintering burrows were difficult to excavate and accurate measurements of most dimensions were not taken. Overwintering burrows were between 20 and 30 cm in depth.

There was no significant difference in volume between cells destined to yield males, and those yielding females (mean volume of cells with male pupae = 1.67 cm³, SD = 0.10, $N = 44$; mean volume of cells with female pupae = 1.169 cm³, SD = 0.09, $N = 13$; $t = 0.09$, $p > 0.9$). This is not surprising because most cells that produced female offspring were reused and had already produced males.

Nests were underdispersed, with mean internest distances in an area with 186 nests averaging 16.9 cm (expected = 26.5 cm; $z = 9.44$, $p < 0.001$). Nests were found disproportionately in areas where the ground was particularly stony (mean number of points touching stones in quadrats with nests = 13.8, SD = 5.6; in quadrats without nests = 10.5, SD = 5.6; $t = 2.7$, $p < 0.01$). Soil beneath stone-covered ground reached a higher temperature during the day and had a higher overall daily temperature than stone-free substrate and soil adjacent to larger rocks (Fig. 3). This suggests that nests are initiated among stones to increase the temperature experienced by developing brood and to reduce development time.

In the analysis of percent weight loss upon drying for soil of the cell cluster and adjacent earth (Table 2), data for the two sampling dates were examined separately because of the great difference in moisture content of both cell cluster and surrounding soil on the two days. On July 11, the moisture content of the soil in the cell cluster was significantly lower than that from adjacent samples (the mean weight loss differential was 14.5%, SD = 4.12, $N = 11$). In contrast, on August 14, there was no significant difference in weight loss between cluster and surrounding soil samples. On the latter date, 4 of

TABLE 1. Nest dimensions for three of the sweat bees investigated in 1987

	<i>A. striata</i>	<i>L. cinctipes</i>	<i>L. comagenense</i>
Turret length (mm)	11.2 ± 5.5 (95)	—	—
Entrance diameter (mm)	3.24 ± 0.32 (98)	—	3.27 ± 0.49 (4)
Burrow diameter (mm)	4.69 ± 0.62 (27)	—	4.85 ± 0.67 (6)
Depth of top of cell cluster (cm)	3.38 ± 1.12 (51)	5.31 ± 1.05* (10)	3.20 ± 1.19 (18)
Depth of bottom of cell cluster (cm)	5.53 ± 1.30 (52)	—	5.48 ± 1.36 (18)
Blind burrow length (cm)	1.61 ± 1.40 (13)	8.17 ± 0.76† (8)	15.1 ± 8.92 (14)

NOTE: Values are given as mean ± standard deviation, with sample size in parentheses.

*Depth of the shallowest cell is given.

†The greatest depth of the nest is given.

14 comparisons showed lower weight loss for cluster soil than for the adjacent sample and the mean differential in weight loss for the entire sample was only 0.13% (SD = 3.02, $N = 14$). The differences in weight loss between sample dates for both cluster and surrounding soil were significant (Table 2), a result of the unusually hot and dry weather between the two sampling dates.

Lasioglossum (Evylaeus) cinctipes

Over 100 nests of *L. cinctipes* were initiated in spring but none successfully produced reproductive brood. Thus, few data could be collected on this species and, because of the unusually small size of the nest foundresses, the nest dimensions provided in Table 1 are unlikely to be representative of the species as a whole.

Unusually for a "carinate" *Evylaeus*, *L. cinctipes* does not construct a cell cluster or a cavity (Figs. 2d, 2e). Nests were underdispersed, with a mean internest distance of 15.3 cm (expected = 20.9 cm; $z = 3.97$, $p < 0.001$).

Lasioglossum (Evylaeus) comagenense

Nest entrances of *L. comagenense* were almost always situated underneath (or on the edge of) stones; it was possible to find nests simply by turning over stones and small rocks in suitable sites. If the stone was on a sloping substrate the nest entrance was usually situated on the downslope side of the stone, perhaps to reduce entry of surface runoff water.

Lasioglossum comagenense is a cavity-building species. The top of the cell cluster of one nest (Fig. 2f), situated beneath a stone, was only 3 mm beneath the soil surface: the top brood cells were plainly visible when the stone was lifted. Blind-ended burrows beneath cell clusters were significantly deeper just before the eclosion of adult brood than during foraging (Table 1; Mann–Whitney U -test, $U_s = 38.5$, $p < 0.025$). The foundress(es) apparently initiated the elongation process before their offspring emerged. Overwintering occurred at depths of 25–35 cm in burrows that were branched near the bottom, but there was frequently more than one female to

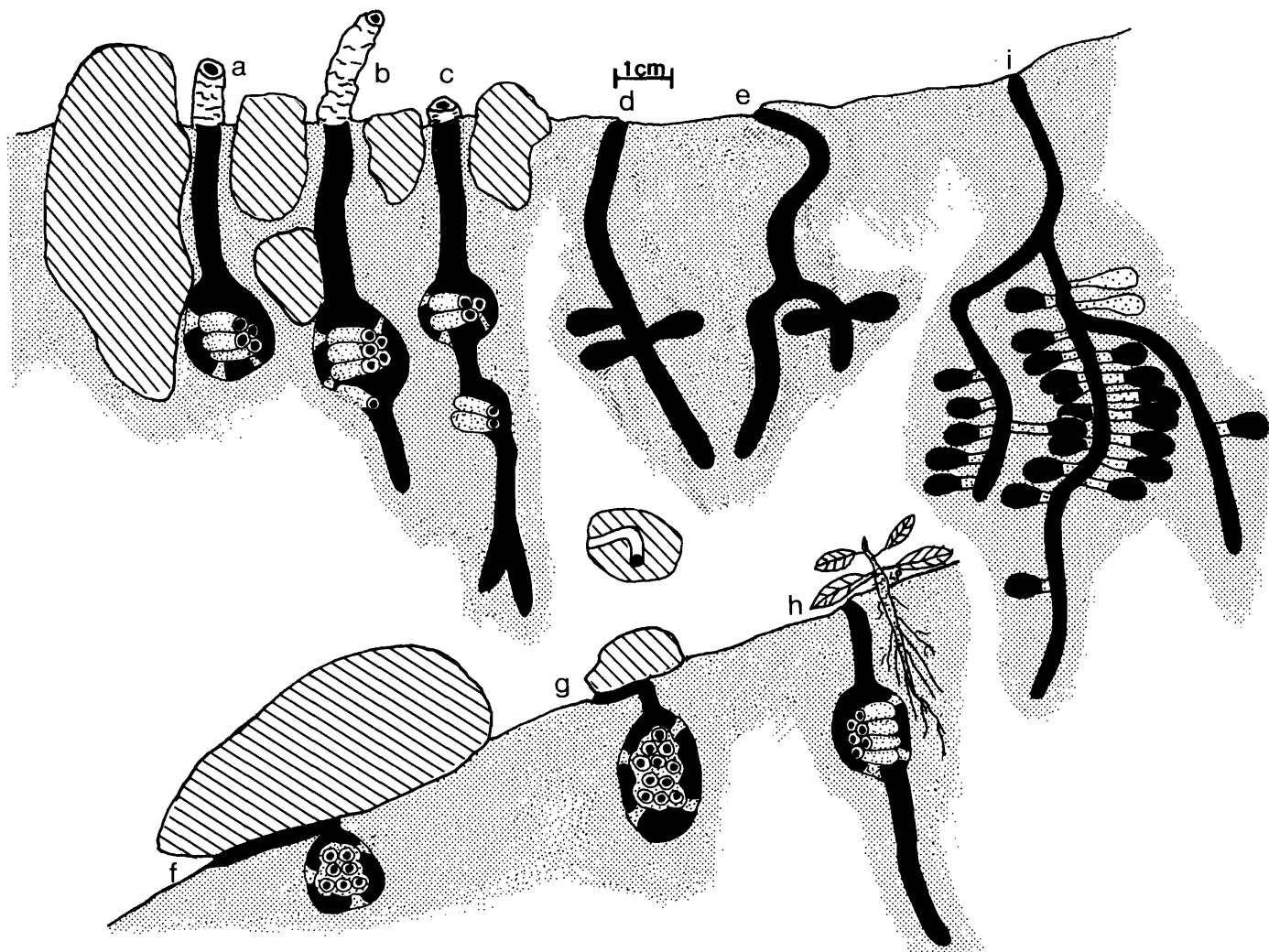


FIG 2. Examples of nest architecture of Cape Breton sweat bees: (a–c) *A. striata*; (d and e) *L. cincitipes*; (f–h) *L. comagenense*; (i) *L. laevisissimum*. Figure 2b shows a nest with one cell constructed on the cavity floor rather than as part of the cluster. Figure 2c shows a nest in which a second, partial cavity was excavated beneath the first cavity; both cells in the second cavity are embedded in the soil of the cavity floor. Figures 2f–2h show the positions of nests beneath surface coverings such as vegetation or rocks. The scale is the same for all drawings.

a branch. Other examples of the nest architecture of *L. comagenense* are given in Figs. 2g and 2h.

Lasioglossum (Dialictus) laevisissimum

Lasioglossum laevisissimum constructs deeper, more meandering nests than the other species (Fig. 2i). This nest architecture is, however, typical for members of the subgenus *Dialictus*.

Brood mortality

Several factors caused brood mortality in *A. striata* and *L. comagenense* (Table 3). Both species had high brood survivorship, however.

Discussion

Nest architecture and social evolution

The relationship between nest architecture and social evolution in halictid bees has been the subject of some dispute. Knerer (1969) suggested that a direct relationship existed between the two, the more advanced social species exhibiting a trend towards gathering the brood cells into a cluster and sur-

rounding them with a cavity. This relationship did not hold when only closely related species were considered (Packer and Knerer 1985). Many exceptions to the purported correlation exist, such as the large cavity forming but solitary *Halictus quadricinctus* (Knerer 1980; Sitkidov 1988) and the apparently advanced social *Halictus hesperus* which does not construct cavities (Brooks and Roubik 1983; Packer 1985).

In the present study, the two species with sessile cells typically had a more advanced social organization than that exhibited by either of the cavity-building species (details of social organization are provided elsewhere: Packer et al. 1989). However, little importance can be attributed to this pattern because (with the exception of *L. cincitipes*) each species exhibits the nest architecture typical of its taxonomic group (genus or subgenus). The absence of a brood cell cluster and cavity in *L. cincitipes* is mysterious, as most other members of the "carinate" *Evylaeus* group construct cavities and *L. cincitipes* is definitely a member of that group (L. Packer, unpublished data). *Lasioglossum (Evylaeus) cooleyi*, another social North American "carinate" *Evylaeus*, also does not construct brood cell cavities (Packer and Owen 1989).

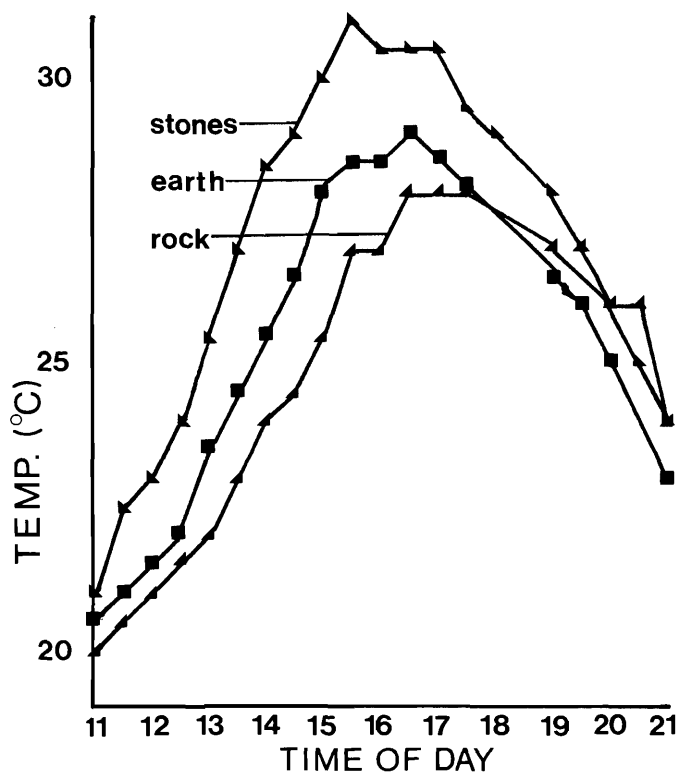


FIG. 3. Variation in temperature 5 cm beneath the soil surface beneath stones, bare soil, or adjacent to a large rock in the *A. striata* study site (measured on July 20, 1987).

In summary, although it is possible that nest architecture has some effect upon social evolution (and vice versa), the relationship is unlikely to be simple.

Some aspects of the adaptive significance of halictid nest architecture

One of the most striking features of the nests of the three species studied in detail is the shallow location of brood cells. The cluster-forming species, *A. striata* and *L. comagenense*, had mean depths at the top of the cavity of only 3.4 and 3.2 cm, respectively. Cavity bottoms averaged 5.5 cm beneath the surface in both species. Comparable data are available for *Lasioglossum (Evyllaes) duplex*, the best known cavity-forming species. In Japan, the mean depth at the bottom of the cavity for 53 spring nests in 1957 was 9.8 cm and for 37 nests in 1958, 8.9 cm (Sakagami and Hayashida 1960). Less detailed data are available for several other cavity-making *Evyllaes* species (Knerer and Plateaux-Quénu 1967, 1970; Sakagami et al. 1982; Packer 1983; Knerer 1983) and all have deeper nests. For *A. striata* in Kansas, Ordway (1966) gives mean depths for the deepest clusters within a nest ranging from 5 to 20 cm depending upon location and time of year (nests were deeper in drier locations and times of year).

Lasioglossum cinctipes, which does not construct a cavity, also had rather shallow cells (mean depth of shallowest cell, 5.3 cm) in comparison with other species with a similar nest architecture (Michener 1966; Michener and Wille 1961; Kirkton 1969; Eickwort and Eickwort 1972; Packer and Knerer 1986).

Taken in their entirety, these data suggest that shallow nests are associated with comparatively moist soils, as is usually the case with sweat bees (Sakagami and Michener 1962). With its

TABLE 2. Moisture content of *A. striata* brood cell clusters and surrounding soil

	% weight loss ($\bar{x} \pm SD$)			
	Cell cluster	Soil sample	t^*	p
July 11	31.92 \pm 0.35	46.51 \pm 0.45	11.63	<0.001
August 14	15.02 \pm 0.27	15.52 \pm 0.13	0.63	>0.5
t^*	9.04	19.8		
p	<0.001	<0.001		

*Statistical analyses performed on angular transformations of the data.

TABLE 3. Mortality factors in two halictine bees from Cape Breton Island in 1987 (numbers in parentheses are percentages)

	<i>L. comagenense</i>	<i>A. striata</i>
No. of cells examined	198	1184
Microbial infection	2 (1.0)	27 (2.3)
Miltogrammine flies	0	3 (0.3)
Rhipiphorid beetles	0	1 (0.1)
Ants	0	18 (1.5)
<i>Sphecodes pimpinellae</i>	0	1 (0.1)
Desiccation	0	15 (1.3)
Unknown	0	18 (1.5)
Total	2 (1.0)	83 (7.0)

maritime climate Cape Breton usually has large amounts of rain during the summer (averaging 44.1 cm for the months May to September inclusive). Shallow nests may be expected under these conditions. However, it has been suggested that drenching of the soil surface could result in brood mortality as a result of cell waterlogging, particularly for shallow brood cells (Packer and Knerer 1986). It is also likely that shallow nests are warmed by the sun to a greater extent than deeper ones. This may be important for populations that are near the northern limit of their geographic range, particularly eusocial species which must complete two brood-rearing phases per season. Additional warming of the brood is provided by the habit of three of the species of nesting in association with surface stones.

The habit of excavating a cavity around the brood cell cluster may serve to increase the rate at which cell soil dries out after rainfall (Packer and Knerer 1986). The variation in moisture content between earth in the brood cell clusters and adjacent soil in *A. striata* nests (Table 2) verifies this suggestion. When the soil was damp on July 11, that in the brood cell cluster lost significantly more weight upon drying than did that of the surrounding earth taken from the same depth. However, in unusually dry conditions, as on August 14, there was no difference in moisture content of brood cell cluster and surrounding soil. It has previously been shown for a halictine species that does not construct cavities that the infection rate of brood cell contents increases after rainfall (Packer and Knerer 1986). Consistent with this hypothesis, brood cell mortality due to infection was very low in both species with brood cell clusters and cavities in the dry summer of 1987. Clearly, more data are required to verify this contention, preferably by experimental manipulation of soil water content.

Why do many halictine species not construct brood cell cavi-

ties? Such cavities are found particularly in the "carinate" species of the subgenus *Evylaeus* and in many of the augochlorine genera (Eickwort and Sakagami 1979). They are conspicuously absent in all small *Dialictus* and "noncarinate" *Evylaeus* species and the larger *Lasioglossum* s.str., *Agapostemon*, and most *Halictus*. Two reasons may be suggested for this difference. Firstly, most species that do not form cavities excavate deeper nests with brood cells at a greater depth than the cavity builders. Flooding of brood cells nearer the surface of the soil is particularly likely after a heavy rain and is much less likely to affect deeper brood cells. Most temperate members of the aforementioned taxa that do not construct cavities position their brood cells at a greater depth than cavity builders. Secondly, a study of intertidal burrowing beetles has indicated that burrows with entrance diameters less than 3 mm are comparatively immune to flooding (Wyatt 1986). This is because the surface tension properties of water require a gap wider than 3 mm for the rapid invasion of burrows by surface water. Thus, nests of the smaller halictines, with narrow burrows (invariably with narrower entrances), may be relatively immune to invasion by surface runoff. This explains the absence of a complete cavity around the brood cells of the smallest "carinate" *Evylaeus* for which the nest architecture is known: *Lasioglossum paucillum* (Packer and Knerer 1985) (it should be noted that an earlier account of the nest architecture of this species (Knerer and Plateaux-Quénu 1967) was based upon a misidentification; the nests described were actually those of *Lasioglossum lineare*) and the small *Dialictus* and "noncarinate" *Evylaeus* species. The absence of a cavity in nests of *L. cinctipes* remains a mystery.

The decrease in *A. striata* foraging activity in late July 1987 almost certainly resulted from the unusually dry soil conditions which are known to preclude cell construction even in species that simply excavate brood cells in the soil rather than constructing them in an already excavated space (Sakagami and Michener 1962). The bees had to await the emergence of their first offspring so that cells could be reused before foraging activity could recommence. The most recently constructed cells in nests excavated in mid-July were often in unusual positions on the floor of the cavity or oriented at 90° to other cells (Figs. 2b and 2c). In addition, the walls of these cells were unusually thin and were impossible to excavate without damage. Similarly unusual cell orientations in nests of this species were observed by Ordway (1966) and also in *L. duplex* by Sakagami and Hayashida (1960). Cells embedded in the bottom of the cavity will certainly require less soil manipulation than the addition of a cell to an existing cluster.

Brood mortality

Individual brood survivorship was high in both *A. striata* and *L. comagenense* (Table 3). However, it should be noted that the data presented for *A. striata* do not include brood cell mortality in those nests for which no surviving immatures or adults were found. The summer of 1987 was unusually hot and dry and apparently some mortality resulted from dehydration and (or) overheating of brood (Table 3). Some entire nests seemed to have completely dried up; for example, on July 11, three nests were excavated that were situated in a thin sandwich of soil between two medium-sized rocks. No brood survived in any of the three cell clusters. Laboratory rearing suggested that the period just before the emergence of adults was the most susceptible to drying out. Upon excavation, some fully developed pupae or recently eclosed adults were

found dead in their cells during the hottest and driest part of the summer. The same nest site choice that resulted in increased developmental rates of brood may have caused offspring mortality from dehydration or overheating in this unusually warm year.

For *A. striata*, the great rarity of nest parasites such as rhipiphorid beetles, the cleptoparasitic *Sphcodes*, and the miltogrammine flies in comparison with generalist predators and edaphic mortality factors (ants, desiccation, etc.) is of interest because these nests, with rarely more than one female in them, were not defended. The possibility that the turret at the nest entrance in this species confers some advantage against insect enemies deserves further attention and experimental manipulation.

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