

The phenology and social biology of four sweat bees in a marginal environment: Cape Breton Island¹

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Augochlorella striata, *Lasioglossum (Evylaeus) cinctipes*, *Lasioglossum (Evylaeus) comagenense*, and *Lasioglossum (Dialictus) laevissimum* were studied on Cape Breton Island, Nova Scotia, throughout their flight season in 1987. The weather during the summer was unusually good, with above-average temperatures and hours of sunshine but very low rainfall. Conversely, the previous summer had been very poor for bees, with comparatively few days suitable for foraging, particularly in July. *Augochlorella striata* was basically solitary but some nests produced one or, at most, two workers, thereby becoming eusocial. In other localities, *L. cinctipes* is known to be eusocial with well-developed morphological and physiological caste differentiation. However, most foundresses observed in 1987 were extremely small, smaller than usual for workers elsewhere, and none of the more than 100 nests produced adult workers or a reproductive brood. Most foundresses were either survivors of the worker brood from the previous year or unusually small reproductive brood females produced as a result of the bad weather in 1986. *Lasioglossum comagenense* was solitary or semisocial with one to four females occupying a nest. *Lasioglossum laevissimum* exhibited significant levels of pleometrosis and an extended period of worker foraging in summer. A comparison of the productivities of these four species indicates the importance of a flexible social system in a marginal climate.

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Augochlorella striata, *Lasioglossum (Evylaeus) cinctipes*, *L. comagenense* et *L. (Dialictus) laevissimum* ont fait l'objet d'une étude dans l'Île du Cap-Breton, Nouvelle-Écosse, durant toute la saison de vol en 1987. Les conditions atmosphériques durant cet été se sont avérées exceptionnellement bonnes : la température était supérieure à la normale, il y a eu un nombre particulièrement élevé d'heures d'ensoleillement et très peu de pluie. En revanche, l'été précédent avait été particulièrement mauvais pour les abeilles, et les jours propices à la recherche de nourriture avaient été peu nombreux, surtout en juillet. *Augochlorella striata* était surtout solitaire, mais certains nids ont produit une, ou au plus, deux ouvrières, ce qui a rendu l'espèce eusociale. En d'autres endroits, *L. cinctipes* est reconnue comme une espèce eusociale et la différenciation morphologique et physiologique des castes y est très marquée. Cependant, la plupart des fondatrices observées en 1987 étaient extrêmement petites, plus petites que les ouvrières originaires d'autres endroits, et aucun des quelque 100 nids n'a produit d'ouvrières adultes ou de reproducteurs. La plupart des fondatrices étaient des survivantes de portées d'ouvrières de l'année précédente, ou des femelles de portées de reproducteurs de taille extrêmement petite à cause des mauvaises conditions de 1986. *Lasioglossum comagenense* était solitaire ou semi-sociale et de une à quatre femelles occupaient un nid. Chez *L. laevissimum*, la fréquence de la pléomérose était significativement élevée et les ouvrières ont été présentes pour une période prolongée durant l'été. La comparaison de la productivité chez ces quatre espèces a mis en lumière l'importance d'un système social flexible dans un climat marginal.

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Introduction

Phenological constraints and sociality

Obligately eusocial Hymenoptera with annual colony cycles living in a strongly seasonal environment are under greater phenological constraints than their solitary, univoltine relatives. This is because social species must interpolate at least one worker brood before producing reproductives, whereas a solitary population with one generation a year only needs one brood-rearing period. The life cycle of a typical univoltine, solitary halictine is as follows. In late summer, males and females leave their natal nests and mate; mated, fed females then enter diapause in a subterranean burrow and initiate new nests the following spring. Halictine females are mass provisioners; they forage and construct pollen balls (one per brood

cell) upon which they oviposit. Each pollen ball provides enough food for the development of one individual offspring. The larvae develop and pupate, and adult males and females emerge, mate, and start the cycle again. The entire process can be divided into three basic stages: (i) nest initiation, (ii) brood development (from cell provisioning until adult eclosion), and (iii) mating plus, for females, preparation for overwintering (Fig. 1a). Of these, brood development takes the most time. Although many halictines are thought to be solitary, the number of species for which this has been adequately documented is small. Examples include *Halictus tsingouensis* (Sakagami 1980) and *Lasioglossum oenotherae* (Knerer and MacKay 1969).

Social halictines with one worker brood normally require two periods of juvenile development to complete their seasonal cycle, one for the worker brood and one for the reproductives (Fig. 1b). In many species, the period between broods is marked by nest closure and bee inactivity. This type of phenology is exhibited by many "carinate" species of the *Lasioglossum* subgenus *Evylaeus* (Sakagami 1974, Michener 1974; Packer and Knerer 1985) and some other halictines such as *Lasioglossum (Dialictus) rohweri* (Breed 1975). Three vari-

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ants of this pattern have been observed. (i) Southern populations of some species, e.g., *L. (E.) malachurum*, have more than one discrete worker brood (Poursin and Plateaux-Quénu 1982; Packer and Knerer 1985). (ii) Nests may be initiated by more than one overwintered female (as a spring semisocial stage in colony development; referred to as pleometrosis). This pattern occurs in many species, including *L. (E.) lineare* (Knerer 1983), *L. (D.) versatum* (Michener 1966), *L. (D.) imitatum* (Michener and Wille 1961), *L. (D.) lineatulum* (Eickwort 1986), and *Halictus ligatus* (Litte 1977; Packer 1986). (iii) Worker foraging activity may result in the production of more workers with a gradual transition from worker to reproductive production. Examples include *L. (D.) versatum* (Michener 1966) and *L. (D.) imitatum* (Michener and Wille 1961). Yanega (1988) has described an additional variant of this pattern, one in which there is a gradual switch from worker to reproductive production within the "worker" brood (that produced solely as a result of foundress foraging).

Figures 1a and 1b illustrate the greater phenological constraints imposed by the simplest pattern of sociality relative to a solitary, univoltine nesting cycle. Figure 1c shows these constraints to be even more severe for bivoltine solitary species, which require extra time for mating and nest initiation between the two brood-rearing phases.

An area may be marginal for a social sweat bee because the duration of suitable weather is barely, but reliably, long enough to support two brood-rearing phases (Fig. 1d, curve x). Alternatively, annual variation in the quality of conditions may be so great that most years are suitable, but poor ones result in local extirpation (Fig. 1d, curve y).

In this paper, phenology, social organization, and productivity are compared for four species of social halictines studied in Cape Breton Island, Nova Scotia, Canada, in 1987. Nest architecture and brood mortality are described elsewhere (Packer et al. 1989). Cape Breton is farther north than any other locality where social halictines have been studied in North America. It is a marginal habitat for social sweat bees because of the high variability in the number of days suitable for foraging activity during what is a comparatively short, and often cool, summer (first and last frosts usually occur in May and September, respectively).

The species observed

Augochlorella striata is known to be primitively eusocial in Kansas (Ordway 1965, 1966; summarized in Michener 1974); *L. cinctipes* is social, with one worker brood and nest closure between brood-rearing phases (Atwood 1933; Knerer and Atwood 1966). Both species are at the extreme northern edge of their range in Cape Breton. *Lasioglossum comagenense* occurs much farther north than the study locality: it has been recorded north of the Arctic Circle (Sakagami and Toda 1986), but its biology has hitherto not been studied. Cape Breton is fairly central in the latitudinal range of true *Lasioglossum laevisimum*, which also extends across North America to the Pacific coast (G. C. Eickwort, personal communication). Batra (1986) described the social organization of a sibling species of *L. laevisimum*.

The weather in 1986 and 1987

Figure 2 expresses various weather data for 1986 and 1987 in terms of percentage deviation from average years. The summer of 1986 was unusually poor for bee activity, especially in July. Conversely, 1987 appears to have been a particularly good year. Although rainfall was above average in June

(largely the result of two big storms), in general the summer was unusually dry; many wells in the neighbourhood dried up.

Methods

In general, nests were located by observing returning pollen-laden foundresses, except those of *A. striata*, which were located by the conspicuous turrets at nest entrances, and most of the *L. comagenense* nests, which were found after a heavy rain which induced surface tumulus construction. For both cavity-forming species (*A. striata* and *L. comagenense*), entire broods were removed from the soil and wrapped in Saran Wrap® for later dissection. Cell contents were examined to determine stage of development, sex, cause of mortality, and other characteristics. Large larvae, prepupae (postdefaecating larvae), and pupae were kept in individual depressions in wax-filled petri dishes until adult eclosion. Pupae were sexed and their head width measured.

Results

Augochlorella striata

The phenology of *A. striata* at Irish Cove is shown in Fig. 3a. Several visits in late May and early June failed to reveal any females where males had been observed the previous autumn. However, by mid-June a few were seen and pollen foraging was well underway by June 21. During the next 3 days over 300 nest entrances were marked. Detailed observations were then made at two dense patches of nests. Foraging continued until mid-July when no bees appeared to be active. Nests were reactivated in early August by the original foundresses ($N = 7$) or by one ($N = 5$) or two ($N = 4$) workers (based upon intensive observation of one nest cluster over a 2-day period). Seventy percent of the nests with surviving foundresses were reactivated.

Before reactivation, the brood sex ratio was biased towards males (523 of 694 censused pupae), and after reactivation, it was biased towards females (9 of 45 pupae). This population is largely solitary, some nests producing one (rarely two) workers.

Before reactivation, nest productivity averaged approximately 6.7 provisioned brood cells ($SD = 2.3$, $N = 28$). Reactivation resulted in 4.5 additional offspring ($SD = 4.1$, $N = 31$; in the above calculations, only nests with surviving foundresses are included). Nests with workers were more productive during the reactivated period than those with solitary foundresses (Mann-Whitney U -test, $U_s = 55.5$, $p < 0.02$).

Lasioglossum (Evylaeus) cinctipes

An approximate phenology for *L. cinctipes* in Cape Breton in normal years, shown in Fig. 3b, is based upon captures and observations made in the Loch Lomond and Irish Cove areas in 1986–1987 and in Glendale (50 km to the west) in 1985 and 1987. Over a period of 17 days starting on May 21, 104 nests were discovered.

Most spring foundresses in 1987 were extremely small for overwintered gynes of this species (mean head width = 2.16 mm, $SD = 0.13$, $N = 37$). Knerer and Atwood (1966) provided wing length data for queens and workers, whereas in the present study only head widths were measured in the field. Wing lengths of Cape Breton females censused in the field were predicted from a calibration plot of head width versus wing length (this procedure was also used to predict wing lengths of pupae excavated from the field that died before eclosion). Most overwintered females were small even in comparison with workers from Ontario, although a few were of normal size for foundresses (Fig. 4).

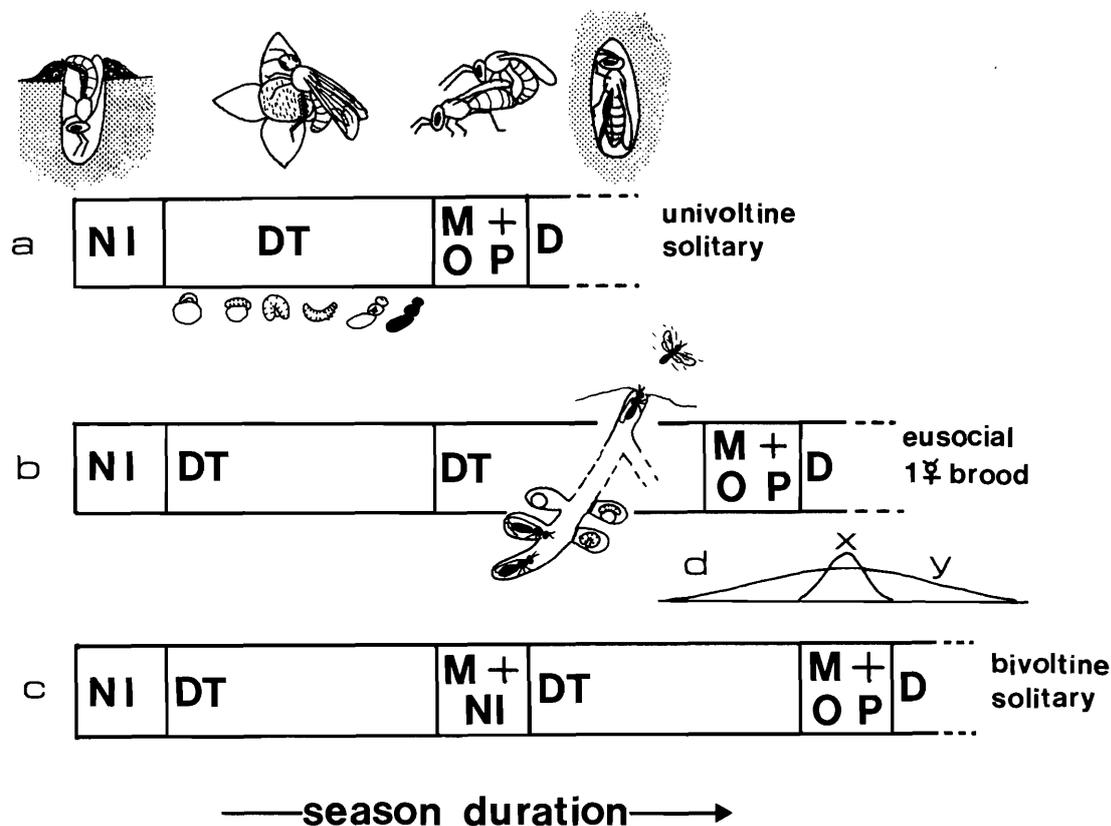


FIG. 1. Phenologies and seasonal constraints of solitary and social halictines. (a) The seasonal cycle of a solitary univoltine population; (b) the seasonal cycle of a eusocial population with one worker brood; (c) the seasonal cycle of a bivoltine solitary species. NI, period of nest initiation; DT, the period required for juvenile development; M+OP, the time required for mating and, for females, preparation for overwintering; D, the beginning of diapause. Relative durations of these phases are generally unknown and little significance should be attached to the exact lengths of the boxes. (d) Variation in timing of the end of suitable brood-rearing weather, x for an area where eusociality is just possible on a regular basis, y for an area where most years are suitable but some are too short (horizontal axis represents date of end of suitable weather, vertical axis represents proportion of years).

Eight workers were collected on July 21 at Glendale. All were of normal size for workers (Fig. 4) (mean head width = 2.18 mm, SD = 0.04). The size difference between workers from Glendale and foundresses from the Salem Road pit was not significant ($t = 0.32$, $p > 0.5$). However, Glendale workers were larger than worker pupae (no adult workers emerged) from the Salem Road Pit (Mann-Whitney U -test, $U_s = 39$, $p < 0.005$).

The high level of wing wear of foundresses excavated from nests in July (mean number of nicks in wing margin = 7.46 ± 5.96 , $N = 13$) was surprising considering the small number of brood cells they had provisioned (mean = 2.07 ± 0.92 , $N = 13$). It is possible that some of the larger, heavily worn, overwintered females in 1987 had also been foundresses in 1986 and that some of the smaller ones had been worker brood individuals the previous year.

Nest excavation data show that pollen balls were constructed in late May to early June and also in early July. Repeated visits during late June indicated that foundresses had ceased foraging for pollen. Nonetheless, no workers were found in the nests that contained pollen balls in July, indicating that the foundresses were responsible for foraging at that time. The data suggest that foundresses were largely unsuccessful in producing worker broods and that some began foraging again in early July. In fact the mean number of cells in nests was slightly greater in June (2.50 ± 1.12 , $N = 4$) than in July! Of the

11 worker brood pupae excavated from nests, 8 were females (72.7%). These daughters were smaller than their mothers, with an average size difference of 6.9% (mother minus daughter head width as a percentage of mother head width). This size difference is less than half that found in Ontario populations of this species (15%, based upon wing length (which is not expected to vary from the figure for head width by more than a few percent); Knerer and Atwood 1966).

Repeated visits to the study site in mid-July to late August failed to reveal any activity at the nest aggregation. A few individuals were collected nearby but none of the study nests produced adult workers and the aggregation was extirpated.

Lasioglossum (Evylaeus) comagenense

The phenology of *L. comagenense* in Cape Breton in 1987 is shown in Fig. 3c. On June 3 at the Salem Road Pit, one nest was observed to have more than one foraging female. The females were marked and the nest was watched for the rest of the day and two bees each made several foraging trips. Upon excavation at the end of the day, a third bee was found within the nest. A second nest was excavated on June 17. Only one marked, active female had been observed foraging. Two females were found within the nest upon excavation in the late afternoon. In each of the above two instances, the nonforaging female had the least wing wear. In the three-female nest the nonforaging individual was the largest, but in the two-female

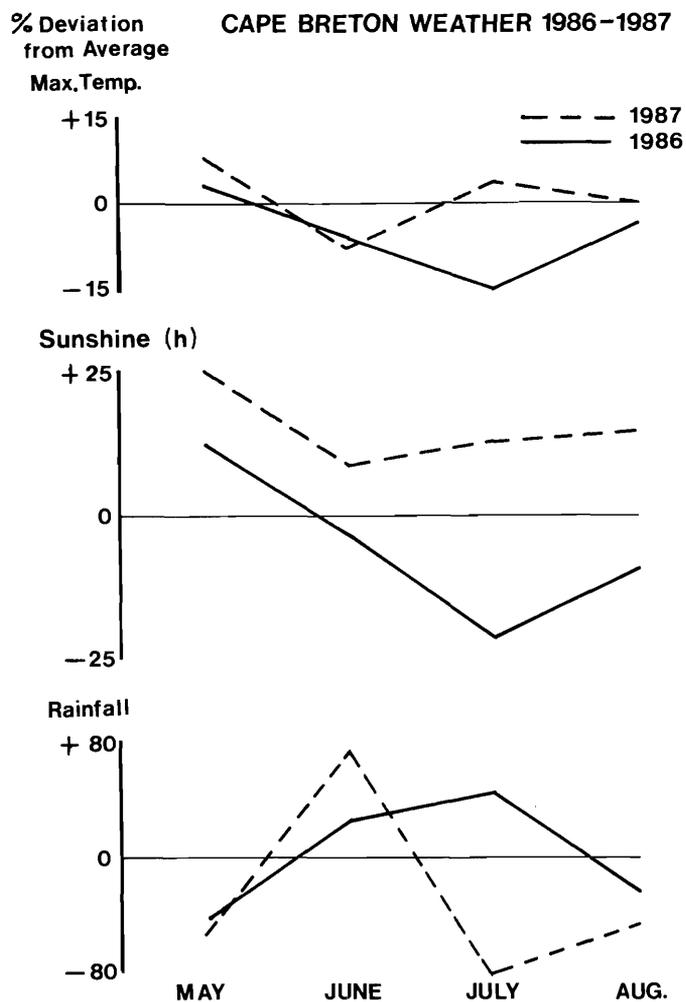


FIG. 2. Percent deviation from normal for various weather factors in Cape Breton in 1986 and 1987, based upon monthly meteorological surveys for Sydney supplied by Environment Canada, Atmospheric Environment Service. Normal weather data are based upon averages for the years 1951-1980 inclusive.

nest she was the smaller bee. All five bees had some ovarian development, but the ovaries of the nonforaging females were better developed than those of their foraging nest mates. There was probably some reproductive division of labour in addition to differences in foraging activity.

Large numbers of *L. comagenense* nests were excavated between July 9 and 13, just before the emergence of adult offspring. From zero to four foundresses were found in these nests. In most multifoundress nests, one or more females had a noticeably lower index of wing wear than the others (mean difference in wing wear index (number of nicks) between the two females in digynous nests = 3.64, SD = 2.36, $N = 7$). Overall, there was high variance in wing wear (mean = 3.77 ± 4.15 , $N = 38$). Nest 14 was unusual in that two of the four females had little wing wear; the other two had a great deal. Perhaps two females in this nest had done little foraging. These data indicate a division of labour between cofoundresses as suggested by the observations of the two nests excavated during the period of foraging activity in June.

Productivities for nests with different numbers of females at the time of nest excavation are given in Fig. 5. Note that the number of foundresses that cooperated earlier in the year will

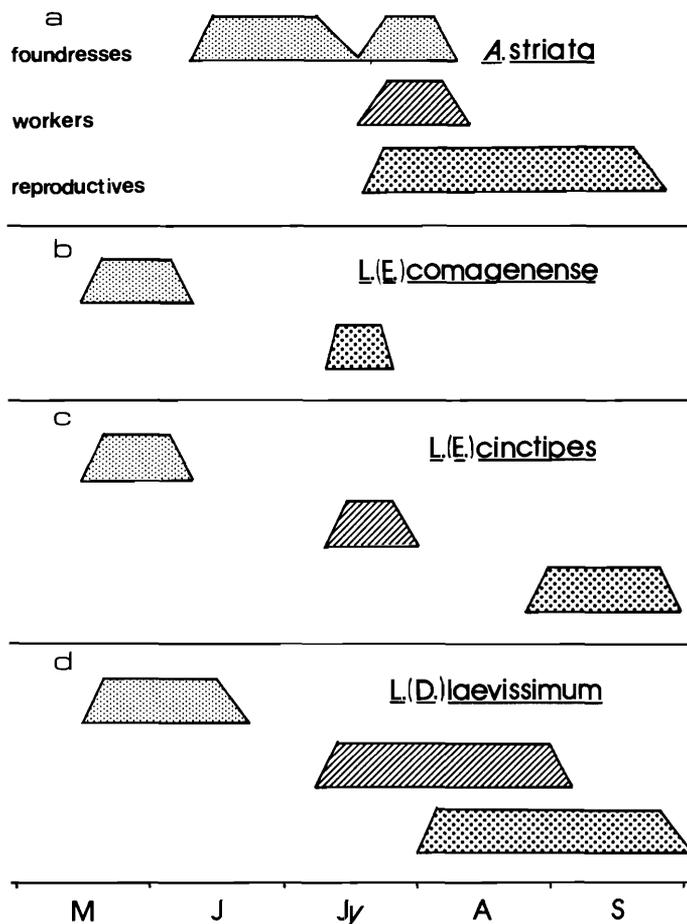


FIG. 3. Phenologies of the four halictine species studied: (a, b, d) based upon detailed records from the study sites in 1987; (c) based upon data obtained from the study site and nearby localities in 1985-1987.

be underestimated with the methods used here: any foundress mortality during the foraging period will be missed except in the two nests excavated in June for which productivity is certainly underestimated. This fact is clearly illustrated by the five nests with brood but no surviving foundresses! In addition, three of the four females in the most productive, apparently single-foundress nests had an index of wing wear far too low for them to have provisioned all of the brood cells alone (inset to Fig. 5). These three nests must have been occupied by at least two females in spring. Productivity of multifemale nests was significantly greater than that of single female nests whether these three nests are counted as having been pleometrotic in spring or solitarily founded (Mann-Whitney U -test, $U_s = 271$, $t_s = 14.9$, $p \ll 0.001$; $U_s = 85.5$, $t_s = 3.16$, $P < 0.01$, respectively).

The period of adult emergence appeared to be remarkably short, much briefer than the foraging period in spring. This was also indicated by the comparatively narrow range of developmental stadia found in nests. Foundress provisioning began in early spring when average temperatures were cool in comparison to those during the last phases of foraging activity. Consequently, the temperatures experienced by the developing offspring produced earlier would have been cooler than those experienced by later siblings. Development of the earlier brood would have been slower in comparison to that of later ones, producing the highly synchronized eclosion of adults.

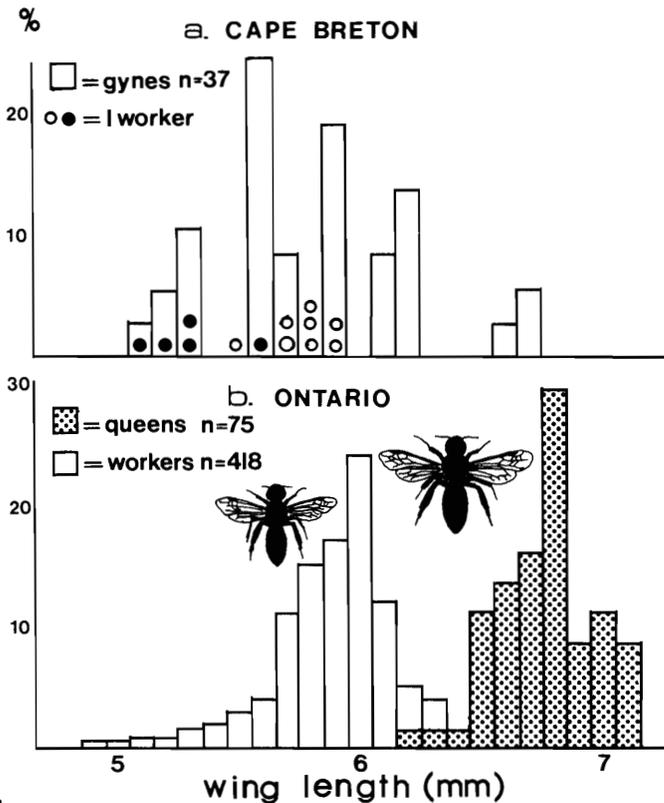


FIG. 4. Size variation in *L. cinctipes* females. (a) Wing lengths of females from the Salem Road Pit predicted from a calibration plot of head width against wing length. Open histograms represent nest foundresses, solid circles represent individual worker brood female pupae excavated from nests, open circles represent individual worker brood adults from Glendale. (b) Wing length data (from Knerer and Atwood 1966) for an Ontario population. Most of the Salem Road females were small, even for workers from Ontario.

Lasioglossum (Dialictus) laevisissimum

The phenology of *L. laevisissimum* in Cape Breton in 1987 is given in Fig. 3d. A small cluster of approximately one dozen nests was observed adjacent to the access road to the Salem Road Pit. In at least three of these nests one female remained at the nest entrance while one or more other females foraged for pollen. One isolated nest found elsewhere was also pleometrotic. Thus, a substantial frequency of pleometrotic nest founding occurs in this population.

Foraging activity continued until towards the end of June and recommenced in early July when workers emerged. This second period of foraging continued into August and some pollen balls were excavated from nests at the end of that month. The duration of worker foraging seemed so long that some offspring resulting from the first worker activity in July may also have become workers. However, this result may have been caused by an extended period of worker production in those nests that were pleometrotic in spring. Nests excavated in late August did not contain overwintering adult females, indicating that diapause does not occur in the natal nest.

Discussion

Augochlorella striata was the last species of the four to become active in spring, 3 weeks or more after the other species began foraging (Fig. 3). Adults or developing brood of the species may require warmer temperatures than those of the

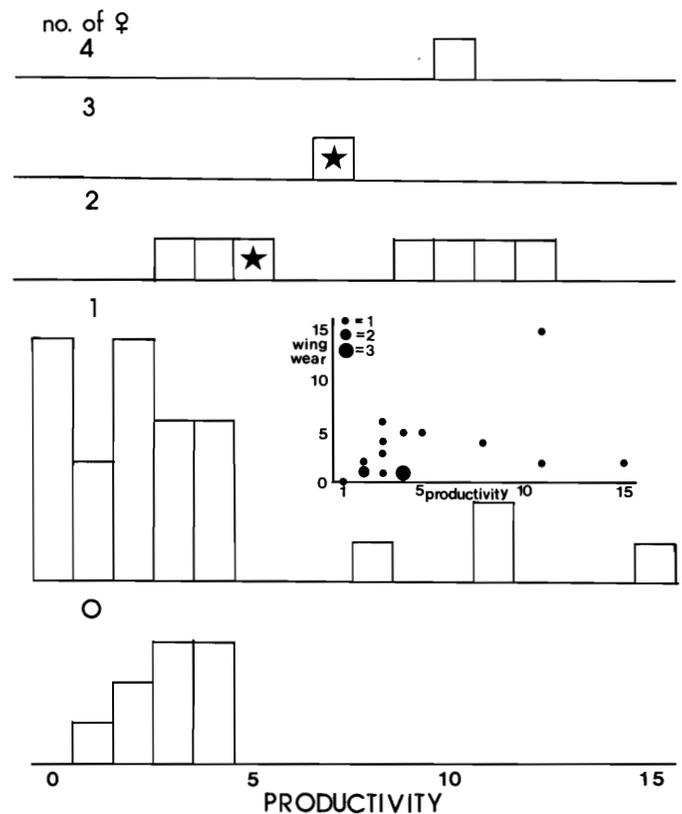


FIG. 5. Productivity (number of brood cells) of *L. comagenense* nests according to the number of foundress females found within the nest at the time of excavation. The two nests marked with stars were excavated during the foraging period in June, and the remainder were excavated after brood production had finished. The inset diagram shows the number of nicks in the wing margin of individual females from single-female nests as a function of nest productivity.

other species. Such a difference would not be surprising as *A. striata* is the most northerly occurring species of its tribe: most members of the Augochlorini are restricted to the New World tropics (Eickwort 1969). Conversely, the other species dealt with here are members of species groups that are generally temperate in distribution. The phylogenetic history of *A. striata* likely renders it the least adaptable to cold climates of the four species studied, irrespective of degree of sociality. In addition to delaying nest initiation, this characteristic likely influenced nest site choice. *Augochlorella striata* nests were found mostly in stone-covered ground and most brood cell clusters were situated adjacent to stones or sandwiched between them. The soil in such situation reached higher temperatures during the day and retained more heat at night than soil in less stony ground (Packer et al. 1989).

The four species discussed in this paper exhibited different types of social organization. *Augochlorella striata* was basically solitary but if one or more of the earliest offspring were females, then some of the foundresses became queens in eusocial nests and (with one exception in which a foundress and a daughter foraged simultaneously) did no further foraging themselves. Less than half of the nests became eusocial and the maximum number of workers was two. A detailed treatment of the social organization of this population and a comparison with data from other studies will be published elsewhere. *Lasioglossum cinctipes* is normally eusocial, with very well-developed morphological and physiological caste differentiation

TABLE 1. Nest productivity of four species of sweat bees from Cape Breton (1987)

	No. of nests	Sociality	Productivity per nest (mean \pm SD)
<i>Augochlorella striata</i>	300	Solitary	6.36 \pm 6.07*
		Eusocial	13.77 \pm 4.76
<i>Lasioglossum comagenense</i>	50	Semisocial	4.8 \pm 3.33
<i>Lasioglossum cinctipes</i>	104	Eusocial (inflexible)†	0
<i>Lasioglossum laevisimum</i>	42	Eusocial (flexible)†	25.0

*Includes those nests in which the foundress died but some brood survived.

†See text for a discussion of these terms.

(Knerer and Atwood 1966). None of the nests of this species discovered in the spring of 1987 produced adult workers and the aggregation was extirpated. Nonetheless, it appeared to have survived with normal-sized workers in other (slightly warmer) parts of the island and in a few scattered nests near the study aggregation. *Lasioglossum comagenense* was solitary or semisocial, with only one brood-rearing period per year. *Lasioglossum laevisimum* is eusocial, with frequent pleometrosis and more or less continuous brood rearing, at least after the emergence of the first workers. Some females produced as a result of the activities of the first workers may also have become workers.

Productivity per nest was highest in the two species with the most flexible social organizations, *A. striata* and *L. laevisimum*, and zero for the least adaptable one, *L. cinctipes* (Table 1). *Augochlorella striata* can be solitary or eusocial and the early females did not always become workers even in 1987, an unusually good year. Under normal or poor conditions perhaps none of the nests become eusocial and all female offspring attempt to overwinter. Similarly, *L. laevisimum* worker brood females may overwinter, perhaps becoming subordinates in multiple-foundress nests the following spring (this suggestion requires verification from more extensive field studies). Certainly the existence of some pleometrotic nests in this population provides evidence of its flexibility in social organization. Multiple-foundress nests of *L. laevisimum* in Alberta (L. Packer and R. E. Owen, manuscript in preparation) were extremely productive in comparison to solitarily founded ones, a situation that has also been recorded for another halictine species (Packer 1986). Additionally, the extended period of worker foraging in multiple-foundress nests will result in increased production of reproductives, particularly in years with an extended foraging season. Such productivity differences may provide an important advantage to pleometrotic nest founding in marginal areas. Conversely, with its colony cycle involving a brood of small workers before the production of males and gynes, *L. cinctipes* appears to be more or less obligatorily eusocial. The small overwintered females observed in 1987 may have been surviving 1986 worker brood individuals and (or) unusually small reproductive brood individuals. Some of the larger females may have been surviving previous-year foundresses attempting to produce a brood in their 2nd year. Nonetheless, *L. cinctipes* has difficulty surviving poor years in this locality; its comparatively advanced eusociality is rather inflexible and local extirpation occurs when species with a more flexible social organization thrive. *Lasioglossum comagenense* exhibits a mixture of solitary and semisocial nests and, thus, should be under the same time constraints as a solitary species. Indeed, semisociality may decrease the time taken to rear a brood of

offspring if the presence of more than one female in a nest decreases the time taken for nest construction or reduces the delay between cell construction and foraging, as has been observed in laboratory studies of another halictine species (Michener et al. 1971). In general, these results indicate that a flexible social structure is advantageous in areas where the duration of the season is highly variable and not always sufficiently extensive to allow two brood-rearing phases.

One way in which the survival of a eusocial population in a marginal environment may be ensured is for some individuals in the "worker" brood to mate and enter diapause without becoming workers. This situation has recently been demonstrated for a population of *Halictus rubicundus* (Yanega 1988). It would appear that *A. striata* (and perhaps also *L. laevisimum*) does this.

Studies of other halictine species indicate that eusociality does not occur in regions where the duration of conditions favourable for foraging is very brief. Thus, a montane population of *L. calceatum* was solitary, even though areas in nearby lowlands harboured eusocial populations (Sakagami and Munakata 1972). Similarly, the montane *Halictus (Seladonia) virgatellus* is solitary (G. C. Eickwort, personal communication) although related species at lower elevations are social.

In general, the data described above indicate that the argument developed in the Introduction (i.e., that eusocial species are under greater phenological limitations than solitary ones) is somewhat oversimplified. Some species exhibit a flexibility in caste determination that enables "worker" brood females to overwinter and become foundresses the following spring. This enables survival in areas with comparatively short flight seasons. Additionally, if "worker" diapause is facultative, influenced by environmental conditions, it could ensure survival in an area where the season is regularly too short for a complete eusocial colony cycle while still allowing the increased productivity that sociality may confer in unusually good years.

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ATWOOD, C. E. 1933. Studies on the Apoidea of western Nova Scotia with special reference to the visitors of apple bloom. *Can. J. Res.* **9**: 443–457.

BATRA, S. W. T. 1986. Ethology of the vernal eusocial bee, *Dialictus laevisimus* (Hymenoptera: Halictidae). *J. Kans. Entomol. Soc.* **60**: 100–108.

BREED, M. D. 1975. Life cycle and behavior of a primitively social bee, *Lasioglossum rohweri* (Hymenoptera: Halictidae). *J. Kans. Entomol. Soc.* **48**: 64–80.

EICKWORT, G. C. 1969. A comparative morphological study and generic revision of the augochlorine bees. *Univ. Kans. Sci. Bull.* **58**: 425–524.

———. 1986. First steps into eusociality: the sweat bee *Dialictus lineatulus*. *Fla. Entomol.* **69**: 742–754.

KNERER, G. 1983. The biology and social behaviour of *Evyllaenus linearis* (Schenck) (Apoidea; Halictinae). *Zool. Anz.* **211**: 177–186.

KNERER, G., and ATWOOD, C. E. 1966. Polymorphism in some nearctic halictine bees. *Science* (Washington, D.C.), **152**: 1262–1263.

KNERER, G., and MACKAY, P. 1969. Bionomic notes on the solitary *Evyllaenus oenotherae* (Stevens) (Hymenoptera: Halictinae) a maternal summer bee visiting cultivated Onagraceae. *Can. J. Zool.* **47**: 289–294.

LITTE, M. 1977. Aspects of the social biology of the bee *Halictus ligatus* in New York State (Hymenoptera, Halictidae). *Insectes Soc.* **24**: 9–36.

MICHENER, C. D. 1966. The bionomics of a primitively social bee, *Lasioglossum versatum*. *J. Kans. Entomol. Soc.* **39**: 193–217.

———. 1974. The social behavior of the bees: a comparative study. Belknap Press of Harvard University Press, Cambridge, MA.

MICHENER, C. D., and WILLE, A. 1961. The bionomics of a primitively social bee, *Lasioglossum inconspicuum*. *Univ. Kans. Sci. Bull.* **42**: 1123–1202.

MICHENER, C. D., BROTHERS, D. J., and KAMM, D. R. 1971. Interactions in colonies of primitively social bees: artificial colonies of *Lasioglossum zephyrum*. *Proc. Natl. Acad. Sci.* **68**: 1241–1245.

ORDWAY, E. 1965. Caste differentiation in *Augochlorella* (Hymenoptera; Halictidae). *Insectes Soc.* **12**: 291–308.

———. 1966. The bionomics of *Augochlorella striata* and *A. persimilis* in eastern Kansas. *J. Kans. Entomol. Soc.* **39**: 270–313.

PACKER, L. 1986. Multiple-foundress associations in a temperate population of *Halictus ligatus* (Hymenoptera; Halictidae). *Can. J. Zool.* **64**: 2325–2332.

PACKER, L., and KNERER, G. 1985. Social evolution and its correlates in bees of the subgenus *Evyllaenus*. *Behav. Ecol. Sociobiol.* **17**: 143–149.

PACKER, L., SAMPSON, B., LOCKERBIE, C., and JESSOME, V. 1989. Nest architecture and brood mortality in four species of sweat bee (Hymenoptera; Halictidae) from Cape Breton Island. *Can. J. Zool.* **67**: 2864–2870.

POURSIN, J. M., and PLATEAUX-QUÉNU, C. 1982. Niches écologiques de quelques Halictinae. I. Comparaison des cycles annuels. *Apidologie*, **13**: 215–226.

SAKAGAMI, S. F. 1974. Sozialstruktur und Polymorphismus bei Furchen- und Schmalbienen (Halictidae). *In Sozialpolymorphismus bei Insekten. Edited by G. H. Schmidt. Wissenschaft Verlagsgesell, Stuttgart.* pp. 257–293.

———. 1980. Bionomics of the halictine bees of northern Japan. 1. *Halictus (Halictus) tsingouensis* (Hymenoptera, Halictidae) with notes on the number of origins of eusociality. *Kontyu*, **48**: 526–536.

SAKAGAMI, S. F., and MUNAKATA, M. 1972. Distribution and bionomics of a transpalaeartic eusocial halictine bee, *Lasioglossum (Evyllaenus) calceatum*, in northern Japan, with reference to its solitary life cycle at high altitude. *J. Fac. Sci. Hokkaido Univ. Ser. VI Zool.* **18**: 411–439.

SAKAGAMI, S. F., and TODA, M. J. 1986. Some arctic and subarctic solitary bees collected at Inuvik and Tuktoyaktuk, NWT, Canada (Hymenoptera: Apoidea). *Can. Entomol.* **118**: 395–405.

YANEGA, D. 1988. Social plasticity and early-diapausing females in a primitively social bee. *Proc. Natl. Acad. Sci.* **85**: 4374–4377.