The social organisation of *Halictus ligatus* (Hymenoptera; Halictidae) in southern Ontario

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The social organisation of *Halictus ligatus* was studied at Victoria, southern Ontario. At this locality, the one worker brood has a protracted period of emergence; this results in small colony populations throughout the summer activity phase. Workers average 12.7% smaller than their queens, 60% of them have some ovarian development, and 42% of them mate. More males are produced towards the very end of the first brood than earlier in the spring provisioning phase. These late first brood males probably survive to mate with reproductive brood females. In orphaned nests, one worker dominates the others to become a replacement queen. Most replacement queens are mated and orphaned colonies produce reproductives of both sexes. Data from this population are compared with those of other studies of this, and other, halictine species.

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L'organisation sociale d'*Halictus ligatus* a fait l'objet d'une étude à Victoria dans le sud de l'Ontario. A cet endroit, l'unique cohorte d'ouvrières a une période d'émergence prolongée; les populations de cette colonie sont donc petites au cours de la phase d'activité de l'été. Les ouvrières sont en moyenne de 12,7% plus petites que les reines, 60% d'entre elles subissent un certain développement ovarien et 42% d'entre elles s'accouplent. Plus de mâles sont produits à la toute fin de l'émergence que plus tôt au printemps durant la phase d'approvisionnement de la colonie. Ces mâles qui apparaissent tardivement au cours de la première reproduction survivent probablement pour s'accoupler aux femelles reproductrices de la cohorte. Dans les nids où il n'y a plus de reine, une ouvrière domine les autres et sert de reine remplaçante. La plupart des reines de remplacement s'accouplent et les colonies orphelines produisent des individus reproducteurs des deux sexes. Ces données sont comparées à celles qui ont été obtenues au cours d'autres études sur cette espèce et sur d'autres espèces d'halictinés.

[Traduit par la revue]

Introduction

Halictine bees exhibit a remarkable diversity of social organisation, with solitary and eusocial species often being found within the same subgenus. The colony cycles of the more advanced eusocial species may be divided into two broad groups. In the first type, periods of complete inactivity separate different brood provisioning phases. This colony cycle is found in the "carinate" members of the *Lasioglossum* subgenus *Evylaeus* (Packer and Knerer 1985). In the second, nests are active from the emergence of the first workers until their demise and the emergence of the last reproductives in late summer or autumn. This type of colony cycle is found in many species of *Lasioglossum (Dialictus)* (Breed 1976), *Halictus* (Knerer 1980), and in some "non-carinate" *Lasioglossum (Evylaeus)* (Knerer 1981). An additional feature, i.e., pleometrotic founding of some colonies, cuts across this classification. Pleometrotic nests of the first colony type will often remain open between spring and summer provisioning phases while the subordinates continue foraging. Pleometrotic nests of the second colony type often remain active from initiation in spring until their demise in autumn.

These two basic types of social organisation present different problems to the student of halictine societies. Bees with bursts of activity separated by periods of nest closure are easier to study. This is because brood development is comparatively synchronized and nest excavation towards the end of the inactive phases will often give a complete picture of brood sex ratio and offspring size. Those species which are continuously active are more difficult to study: a picture of colony development has to be pieced together from data from many nests excavated throughout the colony cycle.

Halictus ligatus is an example of a species that has the second type of colony cycle. Although haplometrotic nests may have a period of inactivity during the development of the first brood, pleometrotic nests do not, and there is continuous activity after worker emergence until the departure of the last reproductive brood individual. Despite there having been more field studies of this species than any other social halictine (Chandler 1955; Kirkton 1968; Roberts 1973; Raw 1975; Litte 1977; Michener and Bennett 1977; Knerer 1980; Eickwort 1985; Packer and Knerer 1986a), much remains to be discovered about its basic biology.

The study reported here was carried out near Victoria, Ontario. Unless stated otherwise, only data from 1984 will be presented here. In 1984, 130 nests were excavated; additional observations at the nest site were made in 1983 and 1985. Analyses of variation in nest architecture of this population of *H. ligatus* have been published elsewhere (Packer and Knerer 1986b) and data on pleometrosis are presented in an accompanying article (Packer 1986). A detailed analysis of female reproductive success and the sex ratio is in preparation.

Methods

The study site was visited several times each week from the beginning of the prenesting phase until the emergence of the reproductive brood. The positions of nests were marked with bamboo skewers with a reference number written on tape at the top. Bees were caught, marked, measured, and released, and nests were excavated as described by Packer and Knerer (1986a). The only methodological difference was that Johnson's baby powder, rather than paprika, was blown down the nest entrances to facilitate excavation.

Traditionally, students of halictine biology count the number of developed ovarioles to gain an estimate of relative fecundity of females. Previous studies of *H. ligatus* (Litte 1977; Michener and Bennett 1977) have distinguished four categories of ovarian development: class A with five or six developed ovarioles, B with three or four, C with one or two, and D with no ovarian development. This procedure

was followed here. Another technique used to judge ovarian development is to measure the width of the most developed oocyte. These methods have been improved upon here by separating developing and resorbing ovariole contents (distinguished by shape and colouration differences) and by estimating the fraction of a whole oocyte present in each ovariole. Fractions of 0, 1/4, 1/2, 3/4, and 1 were estimated by eye. Thus, five scores are available for each female's ovarian development: (*i*) the traditional A to D categorization, (*ii*) the sum total of fractions of whole oocytes that were developing, (*iii*) the sum of resorbing portions of oocytes, (*iv*) the total of *ii* and *iii*, (*v*) the number of fully developed oocytes that were ready to be laid.

The shape of the pollen balls constructed by *H. ligatus* females depends upon the sex and caste that the provision mass will produce (Chandler 1955; Michener and Bennett 1977). Thus, male-producing pollen balls are small, slightly flattened spheres. Gyne-producing pollen balls are elongate and saddle shaped, and have a shallow depression on the dorsal surface to receive the egg. Worker pollen balls are like those of males, but slightly larger. In practice, it is not possible to distinguish male- and worker-producing provision masses on shape and size alone; however, they are produced at different times of year.

Estimates of nest age were made by counting the 1st day that pollen collection was observed in any nest as day 1 and numbering from there. Data from nest excavations were lumped together into 10-day periods for analysis. Categories range from 1 to 9, although an additional sample was excavated on day 116.

The number of nests excavated in each time period is shown at the bottom of Fig. 1. Nests were excavated from at least three different portions of the study aggregation within each 10-day time period. Several adjacent nests were excavated from each portion. These methods avoided bias in the choice of nests excavated within individual time periods.

Results

Description of colony cycle

The bees awake from hibernal diapause in late April or during May. However, they do not leave their overwintering burrows until late May or early June. During warm, sunny days in late May, the gynes that have overwintered may fly to flowers and feed upon nectar and pollen. They establish new nests at this time or return to their natal burrows and refurbish them. Few bees are active on any given day during this period and, as a result, few observations were made.

The first pollen-foraging trips were observed on June 6 in 1983 and June 3 in 1984. Haplometrotic nests were active daily for a period of about 2 weeks and then opened only intermittently until the emergence of the first workers. However, some gynes provisioned one or more cells just before the emergence of the first workers. This resulted in a wide range of developmental stages in some nests excavated just before first worker emergence. Three nests excavated on July 19, when most nests had active workers, contained only the queen, some cells with mouldy contents, and two, three, and four recently provisioned pollen balls with eggs. Thus, each queen had begun provisioning again after the death of her earlier offspring.

The first worker brood pupa was excavated on July 8. The first adult worker was observed on July 16, but because observations were not made for several days before this, some earlier emerging individuals would have been missed. The first reproductive brood male and gyne-producing pollen balls were excavated on July 16. The first reproductive brood male pupa was excavated on July 24 and the first gyne pupa the day after. The first adult young gyne was unearthed on August 22. The last excavations were performed on September 17. Eight nests yielded 8 gyne and 2 male pupae, in addition to 34 adult gynes in their hibernaculae.

The first brood is protogynous, there being significantly more males in the last quarter of the first brood than in the remaining
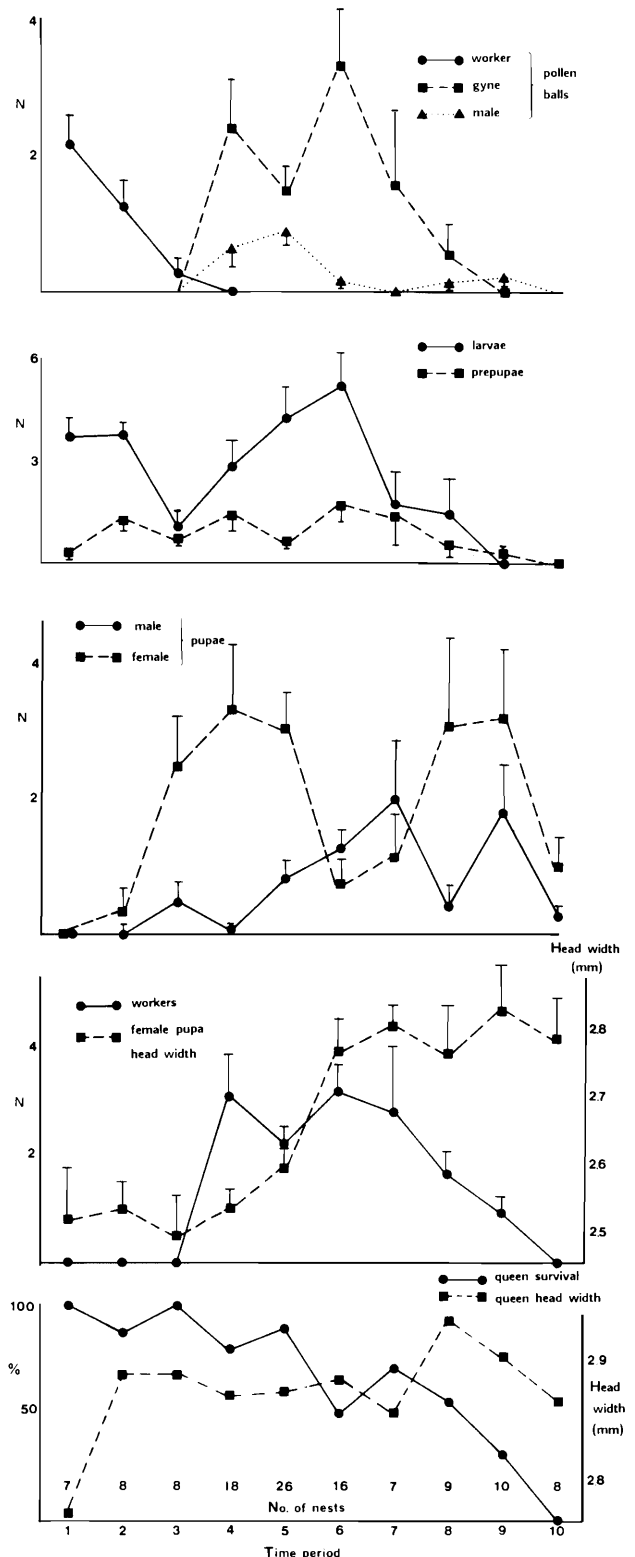

FIG. 1. Variation in brood parameters throughout the duration of the study. Data from haplometrotic, pleometrotic, and orphaned nests combined. For explanation of the different time periods, see footnote to Table 1.

periods together (Table 1). The reproductive brood is protandrous, with significantly more males appearing in the first half of this period (Table 2).

Haplometrotic nests had an average of 6.65 first-brood offspring (SD = 2.6, $N = 20$) with a mean of 5.65 workers per nest; males made up 14.6% of this brood.

TABLE 1. Number of male and female first brood pupae per 10-day period resulting from the spring provisioning phase in haplometrotic nests

Sex of pupa	Time period			
	2	3	4	5
Male	2	4	1	12
Female	17	29	38	48
	$\chi^2 = 4.81$, $p < 0.05$			

NOTE: Time periods refer to 10-day blocks, with time period 1 referring to days 10 to 19 after the 1st day that pollen foraging was observed at the study site. The significance test refers to a comparison of the last time period with the previous three.

TABLE 2. Number of male and female reproductive brood pupae per 10-day period resulting from the summer provisioning phase in haplometrotic nests

Sex of pupa	Time period			
	5	6	7	8
Male	15	14	4	18
Female	12	8	30	32
	$\chi^2 = 13.96$, $p < 0.001$			

NOTE: For explanation of time periods, see footnote to Table 1 and text. The significance test refers to a comparison of the time periods 5 and 6 versus 7 and 8.

TABLE 3. Variation in the proportion of workers with ovarian development and variation in the proportion that had mated in different time periods (see footnote to Table 1)

	Time period			
	4	5	6	7
Ovarian class D	4	15	7	11
Other ovarian classes	17	21	17	6
	$\chi^2 = 9.33$, $p < 0.01$			
Unmated	18	24	8	8
Mated	3	12	16	9
	$\chi^2 = 14.68$, $p < 0.001$			

No new nests were started by worker brood individuals acting independently. It is highly unlikely that any worker-initiated nest would have been missed: all of the nests in the aggregation were excavated by the end of the year and not one nest showed any evidence of being founded by a worker.

Figure 1 shows variation in brood parameters throughout the colony cycle of all nests. As can be seen, male pollen ball production peaked before that of gyne provision masses (occurring on July 31 and August 6, respectively). Female pupa frequency is clearly bimodal, with the first peak representing worker-producing pupae and the second giving rise to young gynes. The variation in female pupa size also reflects this difference, with a sharp increase in mean pupal head width occurring at the end of July and beginning of August.

The percentage of queenright nests falls off gradually during the season, although approximately 70% of the foundresses survive past the peak period of gyne-producing pollen ball construction. Thus, most queens are around for most of the time that the eggs that produce the reproductive brood are being laid. The number of workers alive in the nests remains fairly constant between mid-July and mid-August, but decreases rapidly thereafter. Pollen ball production appears to decline before the worker population falls off. This indicates that the last remaining workers may add little to colony productivity.

Original foundresses were found in 3 out of 10 nests excavated on September 3. At that time, gyne pupae and adult gynes in their hibernal chambers occurred in approximately equal numbers. No original foundresses were found in any of eight nests excavated on September 17. This indicates that queens of this species may have a maximum adult life span of a little more than a year.

Out of a total of 130 nests initiated in spring, 13 (10%) did not survive to produce reproductives. Ten of these 13 nests failed before worker emergence and only 1 is known to have successfully produced workers before it succumbed. Ten of the failed nests were known to have been haplometrotic in spring; the number of foundresses in the remaining three nests was not known.

Workers

The following analyses refer to workers from haplometrotic, queenright (nonorphaned) nests only. Data from 105 such individuals are available from 39 nests in 1984.

Workers averaged 12.7% smaller than their queens, based upon head width. Forty percent of them had undeveloped ovaries (ovarian class D), 49.5% had one or two developed ovarioles (class C), 10.5% had three or four (class B), and none had five or six developed ovarioles; 41.9% of them were mated.

There was significant variation in the frequency of workers with ovarian development at different stages during the summer provisioning period (Table 3, Fig. 2A). Worker ovarian development decreased during the summer provisioning phase (Fig. 2A). That this was not a result of worker ageing can be seen by the lack of correlation between worker age and number of developed ovarioles (Spearman rank correlation coefficient = 0.04, $p > 0.5$).

There was a significant increase in the proportion of workers that had mated as the summer progressed (Table 3, Fig. 2A). This was not due to older bees being more likely to mate ($\chi^2 = 2.3$, $p > 0.05$); rather it probably stemmed from the greater availability of males later in the season. This resulted from the production of some first (worker) brood males towards the end of the spring provisioning phase (Table 1). Additionally, the later workers coexisted with the earlier emerging reproductive brood males: as can be seen from Fig. 1, workers were still active long after reproductive brood male pupae had been produced in the nests. Reduced ability of ageing queens to inhibit worker mating activity could also produce this result. Mated workers were no larger than those that had not mated (mean head width of unmated workers = 2.54 mm, SD = 0.11, $N = 119$; of mated workers = 2.53 mm, SD = 0.11, $N = 72$; $t = 0.32$, $p > 0.5$).

The youngest workers (those with the lowest index of wear) were no different in size from the oldest individuals in the same nest (mean head width of youngest workers = 2.52 mm, SD = 0.09, $N = 31$; of oldest workers = 2.53 mm, SD = 0.11, $N = 48$; $t = 0.21$, $p > 0.5$, the difference in sample sizes results from the number of ties). However, surviving workers in nests after August 12 (day 70) were significantly smaller than those unearthed earlier (mean head width of earlier workers = 2.53 mm, SD = 0.09; of later workers = 2.45 mm, SD = 0.10; $t = 3.47$, $p < 0.005$).
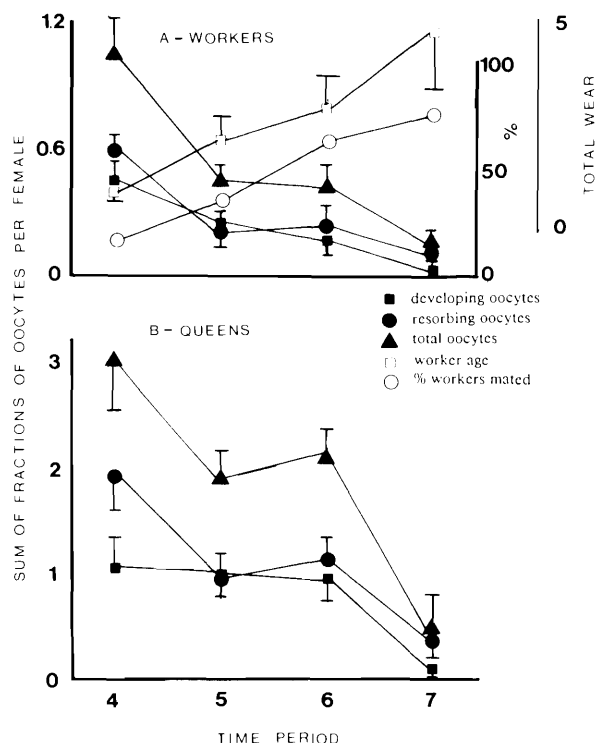
FIG. 2. Variation in reproductive condition of queens and workers during the summer provisioning phase. (A) Workers; (B) queens. Note that the vertical scale differs for the two graphs. For explanation of time periods, see footnote to Table 1.

Workers with the most developed ovaries were not significantly larger than their sisters that had the least ovarian development of any of the workers in the nest (mean head width of most developed workers = 2.56 mm, SD = 0.09, N = 31; of least developed workers = 2.53 mm, SD = 0.09, N = 39; t = 1.22, p > 0.05).

Worker bees that had not been previously observed foraging were compared with foragers excavated from nests. Foragers were no larger than nest workers (mean head width of foragers = 2.51 mm, SD = 0.11, N = 32; of nest workers = 2.52 mm, SD = 0.08, N = 48; t = 0.24, p > 0.8), were no more likely to be worn (χ^2 = 0.98, p > 0.1), and showed no significant variation in presence or absence of ovarian development (χ^2 = 0.17, p > 0.9). They were, however, almost significantly more likely to have mated (χ^2 = 3.39, p = 0.06).

Queens

Queens excavated from nests with brood did not differ in mean size from gynes caught flying in and out of nest entrances during the spring provisioning phase (mean head width of gynes = 2.82 mm, SD = 0.26, N = 111; of queens = 2.85 mm, SD = 0.16, N = 88; t = 0.95, p > 0.2). However, females that overwintered had a higher variance in size than established queens (F ratio = 2.77, p < 0.001). This result is partly due to some of the smaller females being subordinate individuals in pleometrotic nests (Packer 1986).

Queen survival is shown in Fig. 1. Over two-thirds of queens survived until the period of maximum young gyne-producing pollen ball production. Analysis of variance reveals no significant variation in queen size when samples of queens excavated from nests were divided into 10-day time periods. Using t-tests, queens in the first time period were compared with the rest, and those of the last three time periods were compared with the

rest because these were the periods that gave the most divergent gyne sizes. The results were t = 1.86, p < 0.05; t = 1.07, p > 0.3, respectively. This indicates that there was higher mortality of smaller foundresses at the nest initiation stage but thereafter, size had no effect on queen survival.

Figure 2B shows queen ovarian condition during the second provisioning period. As can be seen, the figures for developing oocytes in queens stayed fairly high throughout the first 30-day period, dropping off rapidly thereafter. The figures for queens resorbing oocytes were highest in the first quarter. That this occurred simultaneously with maximal worker ovarian development could reflect reproductive competition within colonies.

Queenless nests

Data are available from 48 workers from 13 orphaned nests. Workers in queenless nests were considered to be replacement queens if they had more ovarian development than any of their sisters. All replacement gynes had more than two developed ovarioles, significantly more than other workers in queenless nests (Fisher's exact test, p = 0.000015), but no different from queens in established nests with workers (χ^2 = 0.21, p > 0.5). Replacement queens were larger than their sisters, but the difference was not significant (head width of working workers = 2.55 mm, SD = 0.11, N = 31: of replacement queens = 2.61 mm, SD = 0.08, N = 9; t = 1.4, p > 0.1). Replacement queens seemed older than their nest mates: significantly more of them were worn than their nest-mate workers (Fisher's exact test, p = 0.0075).

There was no significant difference in relative frequency of different ovarian categories in workers from orphaned and queenright nests, whether replacement queens are or are not included in the analyses (χ^2 = 3.91, p > 0.1; χ^2 = 1.42, p = 0.5, respectively). There were sufficient data to allow comparisons of queenright and orphaned nests only in time periods 4, 5, and 6. The presence or absence of the queen had no significant effect on the frequency of workers with any ovarian development or the proportion that had mated.

There was no significant difference in the relative proportions of male and female reproductive brood pollen balls between haplometrotic, pleometrotic, and orphaned nests (χ^2 = 2.86, p > 0.1). This indicates that orphaned workers can produce female reproductives. Further evidence that this is so comes from the high proportion of mated replacement queens. Replacement queens were more likely to have mated than their orphaned nest mates (Fisher's exact test, p = 0.003). Indeed, only one out of nine such females had not mated. Replacement queens were also more likely to have mated than were workers in queenright colonies (Fisher's exact test, p = 0.006). However, orphaned workers taken together were no more likely to have mated than queenright ones (χ^2 = 0.11, p > 0.5). This may indicate that replacement queens are just as adept at inhibiting worker mating as are the colony foundress queens. Additionally, it appears that mating takes place after a bee has attained replacement queen status in *H. ligatus* as has been shown for laboratory colonies of *L. (D.) zephyrum* (Brothers and Michener 1974; Greenberg and Buckle 1981).

Discussion

Colony development

Litte (1977) made detailed observations at nest entrances. She states that haplometrotic nests were open for 0.8 h a day, with 0.28 foraging trips per hour, and were open for approximately 10 days. This gives a total of only 2.2 foraging trips per

haplometrotic nest during the spring provisioning phase. Clearly this is unrealistic. Some data were obtained on the duration of pollen-foraging trips at the Victoria site. Unfortunately, not all entrances and exits were noticed, making detailed statistical analysis impossible. However, pollen-foraging trips generally lasted from 14 to 25 min with the exception of the penultimate and last trips of the day which were often twice as long. The increased duration of the latter may be due to the collection of both pollen and nectar towards the end of the day. Alternatively, bees may have less motivation for pollen foraging as the provision mass nears completion; they may feed themselves at this time. The duration of these foraging excursions was similar for both gynes and workers, both at this locality and in Florida (L. Packer, unpublished data). It seems probable that gynes collect enough pollen in 1 day to construct one worker-producing pollen ball if the weather is good throughout the active period (approximately 1000 to 1430). In windy, cool, variable, or otherwise marginal conditions, more than 1 day of foraging will be required.

Not surprisingly, the duration of nesting activity varies between localities in *H. ligatus* (Kirkton 1968; Michener and Bennett 1977). At 47° N there are 3.5 months of nesting activity and at 40° N, 5.5 months. The Toronto population (43°40′ N) was active from mid-May until October, approximately 5 months. The Victoria population (43°50′ N), although barely further north, was active for only 4 months, from the beginning of June until the end of September. This difference is probably due to the ameliorating effects of Lake Ontario, the city environment, and the lower elevation upon the temperature experienced by the Toronto population, Victoria being 30 miles from the lake, at an elevation 200 m higher than Toronto. Trees come into bud and the first flowers appear about 2 weeks later at Victoria than within the Toronto city limits and the leaves fall about 2 weeks earlier in the former locality.

Most queens survive until the end of the main reproductive-producing period at Victoria. Thus, once a nest has been established, 70% of the foundresses will remain alive until the peak in gyne pollen ball production has passed. Litte (1977) found that 14.3% of queens had died in July; this figure rose to 43.8% in August.

In the event of queen death, one worker seems to come to dominate the others, both in Ontario and New York. However, Chandler (1955) recorded no replacement queens and found that orphaned colonies produced only male reproductives. This could result from there being no, or very few, males in the first brood in Indiana.

Colony phenology of *H. ligatus* at Victoria follows the "bang–bang" strategy (Oster and Wilson 1978). Indeed, with only one worker brood, this is the only strategy they can adopt. Bulmer (1983) has elaborated upon Oster and Wilson's scheme by showing, theoretically, that colonies should switch from worker to male production and then to queens. Protandry is found in the reproductive brood at Victoria (Table 2), but it is not as clear-cut as the theory may predict. The reason for this is probably the drawn-out period of young gyne emergence at this locality. Thus, late-emerging males may not suffer a greatly reduced probability of finding mates, or high competition from earlier emerged males, if there is a significantly high male mortality rate.

Seger (1983) has suggested that bivoltinism may produce sex ratio biases that favour the evolution of eusociality in Hymenoptera with halictine-like phenologies. Thus, if males from the first brood survive until the emergence of second brood females, the value of second brood males decreases, producing a female-biased sex ratio. The males in the first brood of *H. ligatus* at Victoria appeared disproportionately towards the end of this brood (Table 1). There were significantly more of them in the last quarter of the spring provisioning phase than in the earlier phases combined. This suggests that these males may be destined to mate with reproductive brood females rather than workers or replacement queens. Some of these late males would have emerged only shortly before the first reproductive brood males, indicating that they may successfully mate with females from the next brood. Chandler (1955) reports male longevity estimates of 2 to 2.5 months, more than long enough for first brood males to survive until the emergence of reproductive females. However, it is not possible to state whether this first brood protogyny is a retained primitive character or one that arose after the origin of sociality.

Both Chandler (1955) and Knerer (1980) state that *H. ligatus* has more than one worker brood per year but do not provide any statistical evidence to support this claim. In Toronto in 1964, gynes commenced foraging soon before May 18, a full 2 weeks before that observed at Victoria in 1983 or 1984. The first adult workers observed in Toronto were seen guarding the nest entrances on June 24; at Victoria they would have emerged beginning around July 3. No observations of the Toronto population were made between August 13 and October 1. Workers were still foraging on the former date but only guarded nest entrances on the latter. At Victoria, the last pollen ball was excavated on August 25 and the last remaining worker was observed on September 2. On the latter date, eight workers were excavated from nine nests. The next observations were made on September 27; no workers were found in any of the eight excavated nests.

From these comparisons it can be seen that the evidence for more than one worker brood in the Toronto population is not at all strong. Although one nest excavated on August 13 in Toronto contained four unworn workers, a nest excavated on August 23 at Victoria contained three small, unworn individuals, one of which had been marked as an earlier emerging first brood worker. Figure 3 shows the number of workers excavated from individual nests at different times during the summer provisioning phase of both localities. As can be seen, the patterns are similar, although the Victoria population is comparatively delayed. There was a higher frequency of pleometrosis at Toronto (Knerer and Plateaux-Quénu 1966); this would result in a long spring provisioning phase. Coupled with a drawn-out period of gyne foraging, as observed at Victoria, this would give the false appearance of more than one worker brood. Certainly, more than one worker brood is to be expected in the more southerly regions of the species' range. Unfortunately, data from such regions are sparse (Michener and Bennett 1977; Eickwort 1985). Michener and Bennett (1977) analysed collections of females from flowers. Bees caught in May and from September until November were assumed to be gynes. These were significantly larger than workers collected in August, but not significantly larger than those collected in June or July. However, the spring sample may have contained many smaller subordinates and part of the autumn sample may have contained late-emerging workers. Thus, the head widths of the "gynes" in these samples may be underestimated. The smaller size of later emerging workers contrasts with the results of Knerer (1980), but agrees with those of the present study. Detailed studies of *H. ligatus* from the non-subtropical, southern states would be most welcome.
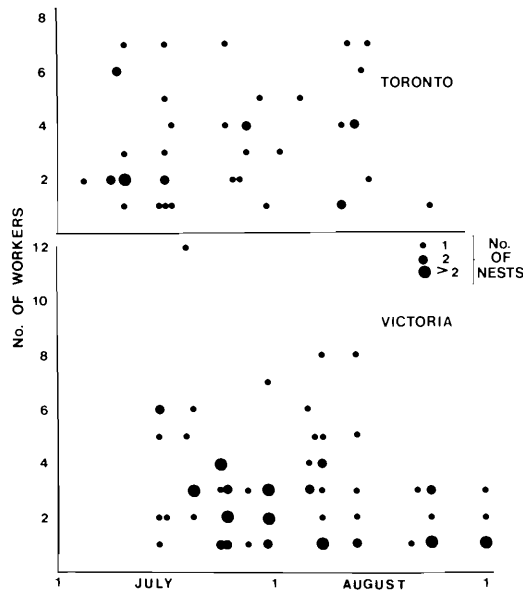
FIG. 3. Number of workers excavated from nests at Toronto and Victoria during the summer phase.

Social level

Interspecific comparisons of social halictine species (Breed 1976; Packer and Knerer 1985) indicate that there is a range of variables that may relate to the degree of sociality in these bees. A reduction in the proportion of males in the first brood, an increase in the mean number of workers, a decrease in worker mating and fecundity, and increased queen–worker size dimorphism are important variables in halictine social evolution. Additional factors that may be important include the frequency of pleometrotic nest associations, the number of worker broods, and the amount of contact between adults and developing immature stages.

Pleometrosis occurs at a low frequency at Victoria and will be dealt with elsewhere (Packer 1986). The number of worker broods has been discussed above. In this section, the remaining six factors will be discussed in reverse order. Data from this population will be compared with those from other studies of temperate *H. ligatus* and with results from other species. In addition, detailed statistics from the Toronto population studied by Knerer (1980) will be provided for the first time. Pair-wise comparisons are made of the three north temperate populations for which the most detailed data are available (Victoria, New York, and Toronto). In making multiple comparisons of subsets of the same overall data, the error rate used has to be modified (Sokal and Rohlf 1981). Thus, in the following statistical tests, significances are quoted after having taken Sidák's multiplicative inequality into consideration (Rohlf and Sokal 1981).

Contact with brood

Only four species of halictine (all of them "carinate" species of the subgenus *Evylaeus*) are known to leave the brood cells open during larval development (Knerer and Plateaux-Quénu 1966). It is probable that periodic opening of cells and inspection of their contents occurs frequently in halictine species, but this is difficult to establish and so far is known only from *L. (D.) zephyrum* (Batra 1964). *Halictus ligatus* gynes with mouldy cell contents begin foraging again before the time that the brood was due to emerge, both in the field and in observation nests in the laboratory (L. Packer, unpublished data). This indicates that there is some contact between adults and immatures in this species.

Morphological caste differentiation

The morphological caste differentiation found at Victoria was 12.7%, based upon head width, and 11.1% based upon wing length. This is a fairly high figure, being exceeded in other temperate halictines only by *L. (E.) malachurum*, *L. (E.) lineare* (Packer and Knerer 1985), and *L. (E.) cinctipes* (Knerer and Atwood 1966). Several tropical species have higher figures: *H. (H.) latisignatus* (Sakagami and Wain 1966), *H. (S.) hesperus* (Brooks and Roubik 1983; Packer 1985), *L. (D.) exiguum* (Packer 1985), and the Damitas population of *L. (D.) umbripenne* (Wille and Orozco 1970). Litte (1977) found a slightly greater dimorphism: 14.4% based upon head width and 12.7% based upon wing length. In Indiana, the figures are much the same as for southern Ontario (12.7 and 12.6% for head width and wing length, respectively (Michener and Bennett 1977)). For Toronto, only wing length measurements are available and the size difference is 14.4%. All these estimates for north temperate populations are very similar. Data from Kansas (Michener and Bennett 1977) indicate a 6.6% caste difference in head width. However, as noted above, this may be an underestimate. Eickwort (1985) found a size difference of only 4.5% between queens and workers of this species in California. Near Bancroft, Ontario, at the extreme northern limit of the species' range, a similarly small figure of 4.8% was obtained (L. Packer, unpublished data). It should be noted that the latter two studies involved very small sample sizes; nonetheless, the small size difference between the castes is surprising.

The reason for the small morphological caste differentiation is probably different for the two localities. In California, the long season of weather suitable for bee activity probably results in the demise of the queen well before the end of the reproductive period. Thus, large workers may have to take over the queen's role. In Victoria, the worker pollen balls are much smaller than gyne-producing ones; they average 43.9 and 66.3 mg, respectively. Thus, workers have to collect pollen and nectar for gyne-producing provision masses that are 50% larger than the ones that produced them. In central Ontario, the length of the flight season is short and weather conditions very unpredictable. Under such conditions, smaller size differences between the castes may be advantageous simply to enable the comparatively larger workers to produce more pollen balls that will result in comparatively smaller gynes.

Worker insemination

The frequency of worker mating increases during the duration of the summer provisioning phase. Litte (1977) found that 5.6% of workers in July and 17.2% in August had mated, whereas for Victoria this proportion increased from 14.3 to over 50% as the season progressed and averaged 42% for the whole period. This is a high figure, being exceeded by few other social halictines: *Augochlorella striata*, *A. persimilis* (Ordway 1965), and Californian *H. farinosus* (Eickwort 1985). For the Toronto population, only 15.9% of the workers had mated, significantly less than in Victoria ($\chi^2 = 15.73$, $p < 0.01$), but not significantly different from that in New York ($\chi^2 = 0.41$, $p > 0.5$).

Worker ovarian development

As indicated in Table 4, 60% of the workers at Victoria had some ovarian development. This is an unusually high proportion, significantly larger than that in either New York or Toronto ($\chi^2 = 26.6$, $p < 0.01$, and $\chi^2 = 18.92$, $p < 0.01$, respectively). The Toronto and New York populations do not differ significantly in this respect ($\chi^2 = 1.72$, $p > 0.1$). This high level of

TABLE 4. Comparison of ovarian development in workers from New York, Victoria, and Toronto

Locality	Ovarian class			
	A	B	C	D
New York	7	12	35	97
Victoria	2	12	72	52
Toronto	0	3	8	33

worker ovarian development is exceeded by no other temperate halictine species, although *L. (E.) nigripes* (Knerer and Plateaux-Quénu 1970), *L. (E.) laticeps* (Packer 1983), and Californian *H. farinosus* (Eickwort 1985) come very close.

The number of workers

The number of workers in the nests stayed fairly constant during the most active part of the summer provisioning phase, varying from 2.8 to 3.4 per nest when divided into 10-day periods. The mean number of workers produced per haplometrotic nest was only 5.6. Litte (1977) found average maxima of 4.3 and 3.4 females alive at any one time, queens included. For Toronto, the mean number of workers from excavated nests was 3.6 (SD = 2.21, N = 52); this is not significantly different from the results from Victoria ($t = 1.15$, $p > 0.2$). Eickwort (1985) excavated two complete haplometrotic spring nests of *H. ligatus* in California. A mean of 11 provisioned cells were found and the gynes were still foraging. Californian populations of this species appear to have a much higher first brood productivity and are worth further investigation. Most haplometrotic halictines average between four and six first brood workers. However, again, Californian *H. farinosus* is an exception. Although the total number of first brood workers in *H. ligatus* in southern Ontario is similar to that found in other haplometrotic halictine species (Breed 1976; Packer and Knerer 1985), the number alive as adults at any one time is small. This is probably a result of more synchronous emergence of workers in other species.

First brood males

Males make up 14.6% of the first brood at Victoria. Neither Chandler (1955) nor Litte (1977) report finding first brood males. However, as pointed out by Knerer (1980), they are easily missed unless a large sample of nests are excavated at the right time. The proportion of first brood males is quite normal for more primitively social halictines as very few species dispense with spring males entirely.

To summarize, *H. ligatus* at Victoria is exceptional in its degree of sociality only in terms of the poor reproductive dominance of queens over workers and the extended period of worker emergence.

As pointed out by Sakagami (1974), Knerer (1980), and Eickwort (1985), members of the subgenus *Halictus* exhibit a similar pattern of sociality with small colonies and comparatively poor reproductive dominance of queens over workers. Although most species have not been studied in sufficient depth to permit detailed comparisons, the California population of *H. farinosus* appears even more primitive, in certain respects, than the Victoria *H. ligatus*: 83% of the worker brood are mated and 53% have developed ovaries. Eickwort (1985) hypothesizes that these high figures reflect the necessity of worker reproduction after foundress death during the long flight season in California. This would explain the large first brood in this species. It is possible that Californian *H. ligatus* has a similar colony cycle. A queen that has a high probability of survival

until the end of the reproductive phase may be selected to maintain low colony sizes to enable more complete dominance over the workers. With a low probability of survival, a queen may increase her fitness by producing a larger worker brood to ensure a larger number of F_2 offspring. In the tropics, the season for bee activity is often even longer. Thus, after queen death, tropical colonies of *H. ligatus* become more or less communal (Michener and Bennett 1977).

In *H. ligatus* from Victoria, most of the queens survive throughout the period of reproductive brood production. Their ovipositional capacities are unlikely to be outstripped by pollen ball production (L. Packer, to be published). It is possible that incomplete domination of workers does enable colonies to produce offspring in the event of a queen's death. However, workers in queenless nests do not have any more ovarian development than those in queenright ones. Replacement queens seem to be quite efficient at dominating their sisters. Thus, it seems unlikely that high levels of worker reproductivity in Ontario *H. ligatus* are caused by the same selective factors as occur in the Californian population of *H. farinosus* studied by Eickwort (1985).

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