

The social organisation of *Lasioglossum (Dialictus) laevisissimum* (Smith) in southern Alberta

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An aggregation of *Lasioglossum (Dialictus) laevisissimum* was studied in Calgary, Alberta, in the summer of 1988. This species was weakly eusocial, with an average of less than 2.5 workers per nest, 43% males in the worker brood, 63% of workers with well-developed ovaries, 35% of them mated, and a mean queen–worker size dimorphism of 7%. Based upon its average rank for these variables, in comparison with eight other species, *L. laevisissimum* is the most weakly eusocial member of the subgenus *Dialictus*. Nonetheless, reproductive-brood production averaged around 25 per nest, and this species is clearly well adapted to short-summer environments. There was little evidence that any worker-brood females entered early diapause rather than functioning as workers. A few spring nests were initiated by more than one overwintered foundress. These pleometrotic nests often had worker-brood productivities that exceeded average reproductive-brood size. Brood mortality was low, infection of provision masses after rainfall being the major factor.

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Une colonie de *Lasioglossum (Dialictus) laevisissimum* a été étudiée à Calgary, Alberta, au cours de l'été de 1988. L'espèce était faiblement eusociale et la colonie comptait en moyenne moins de 2,5 ouvrières par nid, 43% de mâles dans le couvain d'ouvrières, 63% d'ouvrières à ovaires bien développés dont 35% se sont accouplées, et le dimorphisme de taille reine–ouvrière moyen était de 7%. D'après son rang moyen par rapport à ces variables par comparaison avec huit autres espèces, le *L. laevisissimum* est l'espèce la plus faiblement eusociale du sous-genre *Dialictus*. Néanmoins, le nombre de couvains de reproducteurs produit était en moyenne de 25 par nid et l'espèce est visiblement bien adaptée à des étés courts. Aucune femelle issue du couvain d'ouvrières n'a semblé entrer en diapause hâtive plutôt que de jouer son rôle d'ouvrière. Quelques nids de printemps ont été fondés par plusieurs reines hivernantes. Dans ces nids pléométriques, la taille des couvains d'ouvrières excédait souvent la taille moyenne des couvains de reproducteurs. La mortalité au sein des couvains était faible et était due principalement à l'infection des réserves alimentaires après une pluie.

[Traduit par la rédaction]

Introduction

Halictine bees are well known for their diverse social organisation. Because sociality within the group varies greatly even among closely related species, additional field studies are highly desirable. Indeed, the substantial intraspecific geographic variation in social organisation that has been documented (Eickwort and Eickwort 1972; Eickwort 1985; Michener and Bennett 1977; Packer and Knerer 1986a; Packer 1986, 1990; Sakagami and Munakata 1972) suggests that repeated study of the same species may be worthwhile.

Lasioglossum (Dialictus) laevisissimum (Smith) is a member of a group of extremely closely related species, several of which remain unnamed (G. C. Eickwort, personal communication). Batra (1987) presented some information on an undescribed sibling species that is restricted to warmer and generally drier habitats than *L. laevisissimum* s.str. (G. C. Eickwort, personal communication). In Maryland, this species (henceforth referred to as *L. (D.)* sp. near *laevisissimum*) had one worker brood per year, foundresses foraged in late March and April, workers foraged in late May and early June, and mating took place in late June and early July. Each of 12 nests excavated before worker-brood emergence contained only one adult female. A Nova Scotian population of *L. laevisissimum* had a longer colony cycle, with foundress foraging in May and June, worker activity in July and August, and mating from early August until at least the end of September. Approximately one-third of the spring nests in this population were inhabited by more than one overwintered female (i.e., they

were pleometrotic), and in these nests one individual acted as guard while the other(s) foraged (Packer et al. 1989a). Reproductive-brood productivity in the Nova Scotian population averaged around 25, and *L. laevisissimum* was the most productive of the four sympatric halictine species whose biology was compared.

A large, dense aggregation of *L. laevisissimum* nests was discovered on the grounds of the Calgary University Farm in May 1988. To the extent that the bees in the aggregation were found in the same area at the same time, the word population is applicable to them, particularly considering that no other large nesting sites for the species were found in the area despite several days' search. More than 240 active nests were excavated during the summer. This paper describes the social organisation, nest architecture, and brood mortality of this population. Detailed analyses of relatedness and sex investment ratio will be given elsewhere.

Methods

The nesting aggregation was situated in a crescent-shaped area of about 100 m length and 10 m width along the south-facing slope of a partly dried up pond. Most nest excavations occurred before 09:00 or after 18:00, i.e., outside the daily period of foraging activity, to increase the likelihood that all adult nest-mates were collected. I located nests by scraping away the surface soil, thereby exposing the burrow entrances. Talcum powder or differently coloured powdered chalk was blown down nest entrances to facilitate tracing of the narrow meandering burrows in the soil. Nest excavations commenced on June 20th and continued intermittently until August 15th, when no

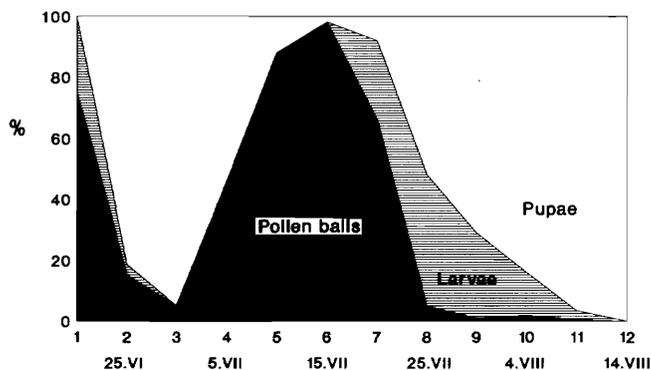


FIG. 1. Percentage of brood found as pollen balls, larvae, or pupae at different times during the summer. Data are broken into twelve 5-day periods, beginning on the dates shown. Data for time period 4 are taken as average for time periods 3 and 5.

nest contained any brood younger than the fully grown larval stage. Whenever brood from adjacent nests may have become confused, data from both nests were ignored.

Fully grown larvae, post-defaecating larvae (commonly incorrectly referred to as prepupae), and pupae were placed in individual depressions in wax-filled Petri dishes and reared to adulthood before being frozen at -80°C . The head width of most pupae and adults was measured with an accuracy of 0.025 mm, using a Leitz Wetzlar microscope with eyepiece micrometer, and a magnification of $64\times$. Ovarian development, spermathecal contents, and wing and mandibular wear of adult females found in nests in July were recorded using standard techniques (Ordway 1965; Packer and Knerer 1986a). Workers foraged only in July, thus data on physiological caste differences are pertinent only for this month.

Percentage size differences between castes are presented as

$$\frac{(q - w) \times 100}{q}$$

where q and w are queen and worker head width, respectively. For some analyses, population-wide averages for queens and workers are compared; in others, queens are compared with each of their workers or with the average for their workers. Statistical comparisons of percent size differences among samples are based on angular transformations of the data. All probability values are from two-tailed tests.

For some analyses, data are broken down into 5-day periods for which the respective dates are indicated in Fig. 1.

In multiple-foundress nests, reproductively dominant individuals were differentiated on the basis of low levels of mandibular and wing wear; queen-like bees typically remain in the nest and thus have comparatively little wing wear and apparently also perform less soil excavation. In addition, inspection of within-nest genotypes at four variable loci helped exclude some individual foundresses as having produced worker-brood eggs (L. Packer and R. E. Owen, in preparation).

Results

Phenology

Overwintered foundresses initiated nests in late May. Most nests were haplometrotic (i.e., initiated by solitary females), but a few multiple-foundress associations (pleometrotic nests) containing up to 5 individuals were found (see below).

Brood production occurred in two discrete phases (Fig. 1): the mostly solitary spring phase, which produced the workers, and the matrilineal summer phase, in which workers provisioned reproductive-brood cells. The first adult worker-brood individuals were excavated on June 26th, the first worker was observed foraging 5 days later, and the first reproductive-

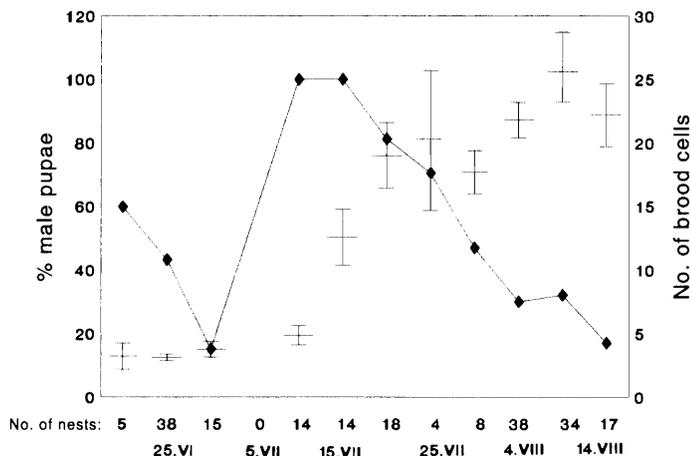


FIG. 2. Percentage of pupae that were male (♦) and the mean (\pm SE) productivity of solitary founded nests (large crosses with error bars) for different 5-day periods.

brood males and females were found on August 10th and 12th, respectively. No evidence indicated that independent nest founding by worker-brood females occurred: no midsummer nests had adult or brood contents indicative of recent founding, and their architectures also suggested earlier initiation.

Average worker-brood productivity in solitary founded nests was less than 5 individuals, and mean reproductive-brood production attained a maximum of around 25 (Fig. 2).

The worker brood

Most nests excavated during the worker-producing period contained some brood that was too young to be sexed (eggs and larvae). Nonetheless, the mean number of females in the worker brood could be estimated in a variety of ways. Only queenright, solitary founded nests are included in the analyses of worker-brood productivity below. Multiplying the mean maximum productivity in the worker brood by the proportion of this brood that was female (see below) gave an estimate of 2.34 workers per nest, but no variance can be attached to this estimate. The actual mean number of female pupae found in worker-brood nests (omitting those nests excavated before most brood had pupated) was 2.04 (SD = 2.7, $n = 45$). However, this value is certainly an underestimate because of brood that could not be sexed. The mean number of workers found alive in nests during the worker foraging period in July was 2.47 (SD = 1.22, $n = 35$). This may also be an underestimate, because of worker mortality during foraging, but it is in closer accord with the first estimate above. It is safe to say that the number of workers produced per solitary founded nest averaged less than 3.

Caste differences

The queen was almost always larger than each worker in its own nest, although there was considerable overlap in population-wide caste sizes (Fig. 3). Head width of queens averaged 1.84 mm (SD = 0.07, $n = 123$), and that of workers 1.72 mm (SD = 0.07, $n = 239$). The average size difference between castes for the whole population was 6.5%. On average, workers were 7.0% smaller than their own queens (SD = 3.7, $n = 239$). Five worker-brood females (less than 2% of the total) were larger than the queens in their nests (Fig. 4), but all had some sisters that were of the usual, smaller size.

Mean worker size declined slightly and mean queen size

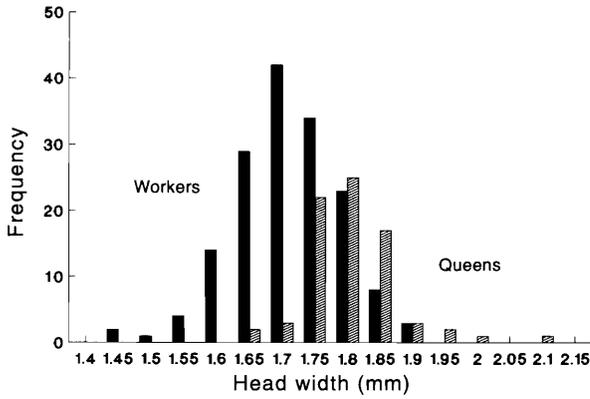


FIG. 3. Size–frequency distribution for queens (solid bars) and workers (cross-hatched bars).

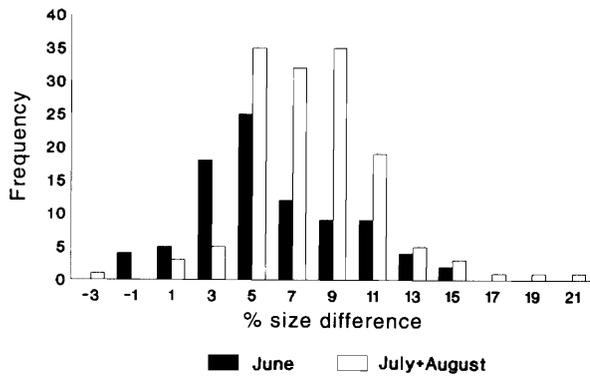


FIG. 4. Distribution of caste dimorphism (estimated as queen head width minus individual worker head width expressed as a percentage of queen head width) for nests excavated in June or later in the summer.

TABLE 1. Comparison of size differences among worker-brood females found at different stages during the colony cycle

	Size (mm)*						% size difference†		
	Workers			Queens			n	Mean	SD
	n	Mean	SD	n	Mean	SD			
June	90	1.73	0.08	30	1.823	0.06	90	5.77a	3.68
July	79	1.72	0.05	46	1.843	0.06	79	7.03b	3.30
August	71	1.70	0.08	34	1.853	0.003	71	8.57c	3.41

*For all pairwise comparisons $p > 0.1$.

†Calculated between each worker and its queen. Means followed by a different letter are significantly different at the 0.05 level (a vs. b) or 0.01 level (a vs. c), based upon ANOVA with Tukey's test.

increased slightly during the year (Table 1). Although none of the pairwise intracaste comparisons were significant, there was a significant increase in caste size dimorphism later in the season (Table 1). There are several possible reasons for this: (i) smaller workers might have been produced later in the worker brood; (ii) larger workers might have had higher mortality rates; (iii) larger individuals may have become replacement queens and thus not categorised as workers; or (iv) larger queens might have produced proportionately smaller workers, resulting in significantly larger caste dimorphism even with a

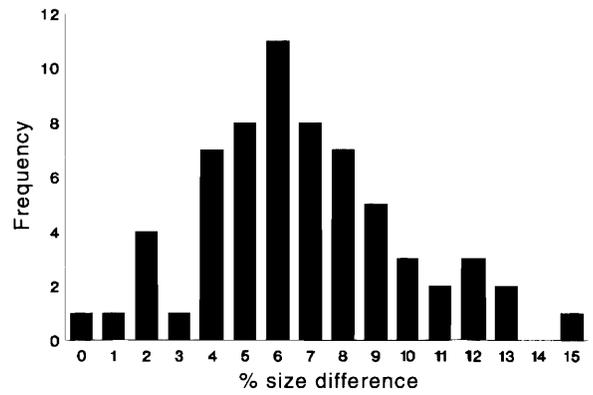


FIG. 5. Distribution of caste size differences expressed as queen head width minus mean worker head width as a percentage of queen head width.

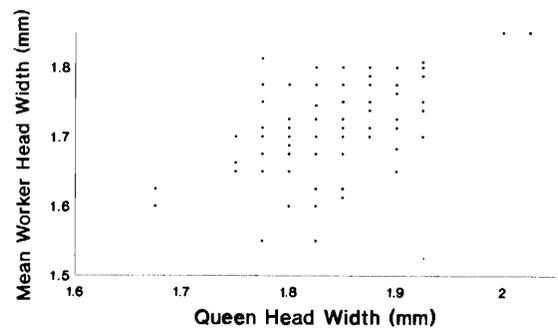


FIG. 6. Scatterplot of the mean head width of workers in each nest plotted against the head width of their queen (for regression equation see text).

slight and nonsignificant increase in mean queen size later in the summer. These four possibilities are assessed as follows:

(i) The increase in mean size difference between queens and workers is not the result of later produced worker-brood females being smaller than earlier ones; the last worker-brood female was the largest worker in 3 nests, the smallest in 4, and of intermediate size in 8 (data from nests with an adequate number of workers whose sequence of emergence could be determined unambiguously).

(ii) If larger bees are more likely to become foragers and smaller ones to perform the less risky intranidal tasks, then higher mortality rates for larger bees may result in a gradual decrease in size of sampled worker-brood females. However, there was no significant size difference between foraging workers and nonforaging nest bees (mean head width for both groups = 1.72 mm, SD = 0.052 and 0.073 and $n = 17$ and 11, respectively, for 7 nests observed intensively for 3 days prior to excavation).

(iii) If replacement queens had arisen from within the worker brood, then small differences may have been expected between the size of a queen and the mean size of its workers. Figure 5 shows the distribution of this variable, for which there is no departure from normality ($g_1 = 0.30$, 95% confidence limits = -0.23 to $+0.94$, $g_2 = 0.59$, 95% confidence limits = -1.03 to $+1.28$). These data suggest that orphaned nests were rare in the reproductive-brood sample.

(iv) Larger queens produce proportionately smaller workers than smaller queens do (Fig. 6). The 95% confidence limits of the slope of the regression of mean worker size against queen

TABLE 2. Size differences in males and workers from multiple-foundress and solitary-foundress nests and between males from worker and reproductive broods

	Size of males (mm)				% size difference (queens - males)				Size of workers (mm)				% size difference (queens - workers)								
	n	Mean	SD	t	p	n	Mean	SD	t	p	n	Mean	SD	t	p	n	Mean	SD	t	p	
Worker brood																					
Solitary-foundress nests	29	1.61	0.07	2.32	<0.05	29	9.78	3.92	1.67	>0.1	54	1.72	0.08	2.13	<0.05	54	5.66	3.54	0.51	>0.5	
Multiple-foundress nests	31	1.65	0.07			31	11.71	3.64			34	1.76	0.07			34	5.79	3.54			
All worker brood combined	60	1.63	0.07	2.97	<0.01	60	11.26	3.80	0.73	>0.4	239	1.72	0.07			239	6.99	3.66			
Reproductive brood	107	1.67	0.09			107	10.74	4.73													

size does not overlap with 1 (the regression equation is $y = 0.56x + 0.67$, $R^2 = 0.30$, and the 95% confidence limits for the slope are 0.39–0.73). Thus, any factor resulting in an increased survival rate of nests founded by slightly larger queens may result in a significant increase in caste size dimorphism over time.

All queens found in nests during the active reproductive-brood production phase in July had some ovarian development, with an average of 3.7 developed ovarioles. Eighty-two percent of the workers ($n = 78$) had some ovarian development, but less than in queens, with an average of 1.8 developed ovarioles. For statistical analysis, bees were placed into one of three categories of ovarian development: 0 or 1, 2 or 3, or 4–6 ovarioles developed. The caste difference in ovarian score was highly significant ($G_{adj} = 42.8$, $p \ll 0.001$). There was no difference in the degree of workers' ovarian development between the first and second halves of the month ($G_{adj} = 0.08$, $p > 0.5$), indicating that workers' ovarian development was not disproportionately high during the peak of male production (Fig. 2). Overall, 63% of workers were considered to have well-developed ovaries, with at least one ovariole containing an oocyte greater than or equal to half the volume of a fully developed egg.

Of all workers whose spermatheca was found (the small size of these bees made dissection rather difficult), 34 ($n = 76$) had been inseminated. All dissected queens had mated.

Production of males

The foraging activity of social halictines is often divided into worker- and reproductive-brood production phases, and the "worker" brood typically contains some males. Of 284 worker-brood individuals excavated as pupae that were sexed, 121 (43%) were male. When corrected for sexual dimorphism in mass (measured as wet weight of eclosed adults), the proportional investment in males in the worker brood was estimated to be 35%. Multiple-foundress nests had a significantly higher proportion of worker-brood males than did solitary initiated ones (56/111 and 65/173, respectively; $G = 4.55$, $p < 0.05$). In singly founded nests investment in males was 30%, and in multiple-foundress nests 43%. For the reproductive brood, 1870 individuals were sexed, of which 599 (32%) were males. This represents an investment of 26% in males. The proportion of males in the worker brood was significantly greater than in reproductive-brood nests ($G = 11.97$, $p < 0.001$). However, the difference becomes nonsignificant when multiple-foundress nests are removed from the worker-brood sample ($G = 2.16$, $p > 0.1$).

Although male and female production overlapped greatly, both worker and reproductive broods were clearly protandrous (Fig. 2).

Size variation among males is summarised in Table 2. Males from pleometrotic nests were significantly larger than those from solitary founded nests. However, the proportional size difference between males and their mothers did not differ between the two nest types. Worker-brood males were significantly smaller than reproductive-brood ones, but again inter-brood variation in percentage size difference between queens and males was not significant. Thus, variation in size of males between broods and nest founding types is probably simply the result of size variation among mothers.

Multiple-foundress associations

Five multiple-foundress nests were excavated during worker-brood maturation: one had 2 foundresses, two had 3, one had

4, and one had 5. An additional nest contained only 1 foundress at excavation but was so productive (28 brood cells) that it must have contained a multiple-foundress association earlier; presumably 1 or more cofoundresses had succumbed before excavation. The arithmetic mean number of females in nests before adult worker eclosion was 1.13 (omitting all orphaned nests) and the harmonic mean 1.04. These nests were astonishingly productive, with an average of 33.3 individuals in the worker brood, almost 10 times as many as in solitary founded nests. Further productivity comparisons between haplo- and pleo-metrotic nests can be found in Packer (1992).

Dominant cofoundresses were slightly larger than subordinates, which were, in turn, larger than solitary nesting females (head widths were as follows: dominant cofoundresses, 1.86 mm, SD = 0.043, $n = 6$; subordinates, 1.83, SD = 0.074, $n = 11$; solitary foundresses, 1.81, SD = 0.055, $n = 26$). However, analysis of variance with multiple pairwise comparisons revealed no significant size differences.

Workers in multiple-foundress associations were significantly larger than those in solitary founded nests (Table 2), but as with males, the proportional size difference between workers and their mothers did not differ significantly between nest types.

The large number of worker-brood individuals produced in multiple-foundress nests was not only the result of a higher rate of brood production. Multiple-foundress nests had a more extended period of worker foraging: during the 4-day period when all six multiple-foundress nests were excavated, 44 brood were younger than the fully grown larval stage, whereas in 52 solitary founded nests only 16 brood were as young. Multiple-foundress nests could be continuously active from initiation until the last worker stopped foraging. Thus, worker and reproductive broods intergraded imperceptibly in these nests. It is quite likely that many of the later "worker"-brood individuals produced in multiple-foundress nests were actually reproductives. Further observations are required on this.

If any multiple-foundress nests were excavated during reproductive-brood production, they were not as productive as may have been predicted on the basis of their populous worker broods (Fig. 7).

Nest architecture

Lasioglossum laevisimum has a typical nest architecture for a member of the subgenus *Dialictus*, with sessile brood cells arising from narrow, branching burrows. An example is shown in Packer et al. (1989b). The only unusual features observed in the nests in Calgary were just beneath the entrance. When the surface soil was at its driest and most powdery, secondary constrictions of the nest burrow were constructed at the depth where the soil became firm. These were especially obvious because the main burrow in reproductive-brood nests is expanded just beneath the surface, presumably to allow bees to pass one another easily near the entrance. In nests with a secondary constriction, this expanded portion occupied the entire distance between the entrance and the constriction below. The constrictions presumably served to inhibit the entry of loose soil or, after a heavy rain, water or mud.

Summary statistics for the architectural features of nests are provided in Table 3. Wider nest entrances and main burrows might be expected when the larger queens are the only bees doing the foraging, as was found in *Halictus ligatus* (Packer and Knerer 1986b). However, in *L. laevisimum*, entrances and main burrows were wider during reproductive production.

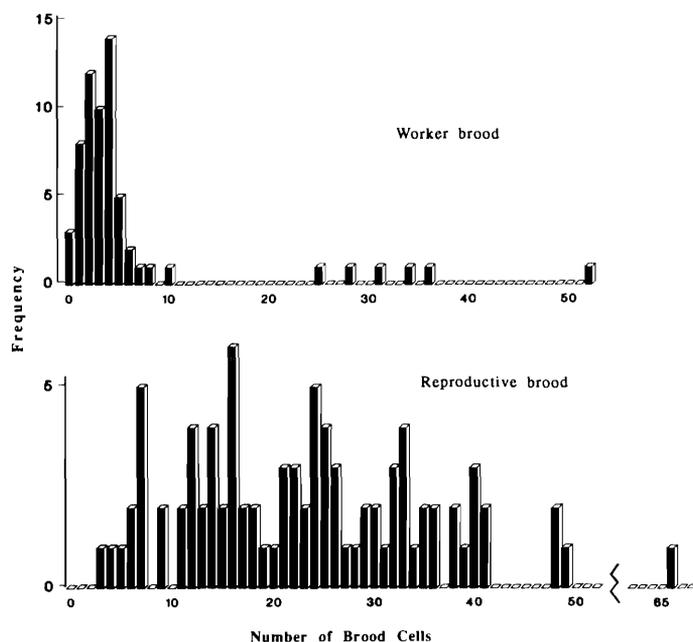


FIG. 7. Numbers of individuals in worker and reproductive broods. (Redrawn from Packer 1992.)

Although nests are significantly deeper later in summer, the depths of the shallowest active cell (i.e., containing brood) did not differ between broods. This suggests that new reproductive-brood cells are excavated at a wide range of depths, some of them interspersed among worker-brood cells.

Mortality

Only six nests with no living occupants were discovered. Considering the methods used to locate nests, this is likely to be an underestimate of the true proportion of failed nests because unoccupied burrows soon became filled in with loose soil. Two of these six nests had been considerably damaged by earthworms. Six worker-brood nests contained an adult foundress but no brood. The reasons for such foundress dysfunction remain unknown.

Seven percent out of a total of 340 worker-brood cells and 3.5% out of 2466 cells for the reproductive brood showed evidence of brood mortality. The causes of death are summarised in Table 4.

Infection of provision masses was the largest single mortality factor, being responsible for 76% of the total. Comparison of observed and Poisson expectation frequencies of 0, 1, and more occurrences of mouldy cells within nests shows that infections were contagiously distributed among nests (Table 5). This result is not due to high infection rates in nests with few adult occupants; indeed there were significantly more females in worker brood production phase nests that contained one or more mouldy cells than in those that did not (mean number of females in nests with a mouldy cell = 2.11, SD = 1.45, $n = 9$; mean number in uninfected nests = 0.79, SD = 0.51, $n = 66$; $t = 5.48$, $p < 0.001$). There was no difference in the mean numbers of adult females in reproductive-brood nests that were infected or uninfected (mean = 2.40, SD = 1.58, $n = 113$; mean = 2.11, SD = 1.58, $n = 50$, respectively; $t = 1.08$, $p > 0.2$).

Previous analyses (Packer and Knerer 1986b; Packer et al. 1989b) have suggested that brood mortality due to mould

TABLE 3. Summary statistics for architectural traits of nests for worker and reproductive broods

	Entrance diameter (mm)			Burrow diameter (mm)			First cell depth (cm)			Total depth (cm)										
	<i>n</i>	Mean	SD	<i>t</i>	<i>p</i>	<i>n</i>	Mean	SD	<i>t</i>	<i>p</i>	<i>n</i>	Mean	SD	<i>t</i>	<i>p</i>					
Worker brood	10	1.92	0.40	2.84	<0.01	11	3.2	0.60	3.16	<0.01	14	5.5	0.75	0.03	>0.9	26	9.7	2.54	3.83	<0.001
Reproductive brood	29	2.29	0.34			30	3.67	0.34			39	5.51	1.09			43	14.3	5.74		

TABLE 4. Factors causing mortality of worker and reproductive broods

	Worker brood		Reproductive brood	
	No.	%	No.	%
Miltogrammines	6	1.8	6	0.2
Bombyliids	9	2.6	2	0.1
Mould	7	2.1	76	3.0
Red discolouration	1	0.3	3	0.1
Total	23	6.8	87	3.5

NOTE: The total number of brood cells was 340 for the worker brood and 2466 for the reproductive brood.

TABLE 5. Numbers of nests containing various numbers of mouldy brood cells in reproductive-brood nests

No. of mouldy cells	No. of nests observed	No. of nests expected
0	89	68.05
1	19	41.38
2	13	12.58
3	3	2.55
4	3	0.39
5	2	0.05

} 21 } 15.26

$\chi^2 = 19.13, p \ll 0.001$

NOTE: The χ^2 value was calculated using data for 2 or more mouldy cells combined (df = 2).

increases after rain as a result of infection following cell waterlogging. The weather in 1988 was slightly warmer than usual and quite dry from May until the end of July. On August 1st there was 6.5 cm of rain, 1 cm above the normal total monthly rainfall (data from monthly meteorological summaries for Calgary from Atmospheric Environment Service, Environment Canada, available from the author upon request). Consequently, both the proportion of cells with mouldy contents and the proportion of nests containing one or more infected cells were compared between nests excavated during the earlier dry period and after August 1st. Before August 1st, 14 out of 1243 cells in 9 out of 147 nests had mouldy contents; after that date 69 out of 2147 cells from 37 out of 93 nests contained mould. Whether the numbers of cells or numbers of nests containing one or more mouldy cells are compared, there was a significantly higher infection rate after heavy rain ($G = 16.04, p \ll 0.001$ and $G = 27.86, p \ll 0.001$, respectively). Although this result should be interpreted with caution, it is in agreement with data on other species which showed that increased infection rates followed high rainfall at various times of year (Packer and Knerer 1986b; Packer et al. 1989b).

Eleven bombyliid larvae were found associated with *L. laevisimum* nests. Previous research (Packer 1988) suggested that these larvae may consume more than one host in order to complete development. This is even more likely with the small *L. laevisimum* as host, and total mortality due to this agent is probably underestimated here.

Four dead larvae of a deep red colour were found. Batra (1965) found the bacterium *Serratia marcescens* to be the cause of similar discolouration in larvae of *Lasioglossum (Dialictus) zephyrum*.

TABLE 6. Data comparing the social biology of eight *Dialictus* species

	<i>zephyrum</i>	<i>rhytidophorum</i>	<i>rohweri</i>	<i>versatum</i>	<i>imitatum</i>	<i>umbripenne</i>	<i>lineatulum</i>	<i>laevissimum</i>	sp. near <i>laevissimum</i>
% workers mated	8.0	12.9	37.9	3.0	2.5	2.5	20.0	35.0	na
Rank	5	4	1	6	7=	7=	3	2	—
% queen-worker size difference	9.1	6.0	10.0	11.9	9.9	16.9	4.4	7.0	9.0
Rank	5	2	7	8	6	9	1	3	4
% workers fecund	38.0	28.0	9.0	25.0	12.0	32.0	28.3	63.3	53.6
Rank	3	6	9	7	8	4	5	1	2
No. of bees per nest	14.3	3.8	4.9	29.6	8.1	75.6	7.0	3.5	6.7
Rank	7	2	3	8	6	9	5	1	4
% males in first brood	14.0	41.0	0.0	5.0	0.0	8.0	25.0	42.6	0.0
Rank	4	2	7=	6	7=	5	3	1	7=
Mean rank	4.8	3.2	5.4	7.0	7.1	6.9	3.4	1.6	4.4

One of 89 workers contained a conopid larva in its abdomen in July.

Discussion

Lasioglossum laevissimum has a typical nest architecture for a member of the subgenus *Dialictus*. The only difference between this and other *Dialictus* species is the narrowness of the secondary constriction beneath the nest entrance. The brood mortality data support previous observations of low death rates among sweat bee brood, the major factor being infection probably resulting from cell waterlogging (Packer and Knerer 1986b; Packer et al. 1989b). This lends further support to the view that the function of the waxy, waterproof cell lining produced by the Dufour's gland (see Cane 1983) of halictid females may not be to maintain a high humidity within the brood cell but rather to keep excess moisture out.

Comparative social biology of *Dialictus*

The taxonomic distribution of eusocial and solitary species among various halictine genera and subgenera suggests that eusociality has originated within this group many times independently. Even within the subgenus *Dialictus* there are half a dozen species-groups that are eusocial, a similar number in which only solitary behaviour has been observed, and a couple that exhibit both types (G. C. Eickwort, personal communication).

A comparison of the social organisation of *L. (D.) laevissimum* with that of other *Dialictus* species is provided below. Only variables that have been estimated for half a dozen or more *Dialictus* species in the field will be discussed. Breed (1976) summarised the information on *Dialictus* species available at that time. Since then, Eickwort (1986) has studied *Lasioglossum (Dialictus) lineatulum*, and Batra (1987) has studied *Lasioglossum* sp. near *laevissimum*. Comparative data for these eight species and *L. laevissimum* are presented in Table 6.

Lasioglossum laevissimum is the most weakly eusocial species included in Table 6, as suggested by its low average rank for the included variables. The comparison between true *L. laevissimum* and its sibling species studied by Batra (1987) provides some interesting insights. The population studied by Batra produced no males in the worker brood and had more than twice as many bees in worker-brood nests, both indicative of a more advanced sociality. However, the caste size differ-

ence in the species studied by Batra was only slightly greater than that in *L. laevissimum* reported here, and the proportion of workers with well-developed ovaries was similarly high for both species. Indeed, Batra suggested that workers are probably responsible for laying most, if not all, the haploid eggs in the more southerly species.

Calgary *L. laevissimum* received the lowest rank for the number of adult females active in the colony and the proportion of males in the first brood. These two variables may not be entirely unrelated because, for a worker brood of a given size, the number of workers necessarily decreases as the proportion of males produced increases. Possible reasons for this high level of male production are discussed below.

It is thought that worker-brood males are produced to mate with replacement queens. However, there seem to be very few replacement queens in *L. laevissimum*. Perhaps these males are destined to mate with reproductive-brood females. If so, we would expect an increase in male production towards the end of the worker brood, as has been noted in *H. ligatus* (Packer 1986). However, the reverse is the case (Fig. 2).

Another possibility is that the males mate with worker-brood females which then go into early diapause without having behaved as workers. This phenomenon has been referred to as brood divalency by Yanega (1988), and we now turn to a discussion of the possibility of its occurrence in Calgary *L. laevissimum*.

Brood divalency

Lasioglossum laevissimum has one worker brood per year. Its geographic distribution does not extend very far south, although it is replaced in more southerly locations by one or more sibling species. This species' success in high-latitude, short-summer environments may result from caste plasticity such that worker-brood females facultatively overwinter in bad years rather than becoming workers (Packer et al. 1989a). Such brood divalency was recently described for *Halictus rubicundus* (Yanega 1988). In *H. rubicundus* the proportion of males in the worker brood increases gradually in spring, and the later emerging worker-brood females are more likely to mate within a few days of emergence as the summer progresses. There is also a gradual increase in female size as the season progresses. Yanega suggests that early mating triggers early diapause, although this suggestion requires experimental support. Detailed observations of a large number of indi-

vidually marked bees over at least 2 years are required to demonstrate conclusively that early-diapausing females occur. Nonetheless, some indirect evidence can be brought to bear on the subject.

Three predictions can be made if brood divalency were occurring.

1. Fewer workers will be found working in nests than expected on the basis of earlier excavations of worker-brood pupae. As described above, accurate estimation of the number of worker-brood females produced was difficult. Multiplying the best estimate of mean worker-brood size by the proportion of females found in this brood gave a figure of 2.3 worker-brood females per nest. This is not significantly different from the mean number of workers found working in 11 nests excavated just after the last worker-brood individuals had eclosed (mean = 2.64, 95% confidence interval = 1.96–3.32).

2. Comparing the size distribution of adult workers with those excavated as pupae should indicate that larger individuals opted out of subservience. Worker-brood females excavated as pupae were more similar to their queen in average size than workers found working in nests later in the year, and there was a gradual decrease in worker size relative to the queen as the summer progressed (Table 1). However, there was no significant difference in the proportion of females similar in size to the queen between worker brood excavated as pupae and those found working in the nest later (5 out of 88 bees excavated as pupae were similar in size to the queen versus 3 out of 138 found later; $G_{adj} = 1.86$, $p < 0.1$).

3. The size distribution of overwintered females should have an inflated lower tail indicative of the presence of some early-diapausing worker-brood females from the previous year. The size distribution of overwintered females is shown in Fig. 3. There is significant skew in this distribution ($g_1 = 0.58$, 95% confidence limits = 0.16–1.01), but the positive g_1 indicates skewness to the right rather than to the left. Thus there is no evidence for an inflated left-hand tail to the size distribution, as would be expected if some overwintered worker-brood females had been included in this sample.

Thus, there is at best weak evidence to support the existence of early-diapausing females in this population. Long-term studies of this species are required to confirm this.

In conclusion, *L. laevissimum* appears to be the most primitively eusocial *Dialictus* species for which published data are available. This primitiveness is indicated not only in terms of small colony sizes (which may, ultimately, merely reflect the short summer season at the study locality) but also in the large proportion of workers that were mated and had undergone ovarian development.

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- Batra, S. W. T. 1965. Organisms associated with *Lasioglossum zephyrum* (Hymenoptera: Halictidae). *J. Kans. Entomol. Soc.* **38**: 367–389.
- Batra, S. W. T. 1987. Ethology of the vernal eusocial bee *Dialictus laevissimus* (Hymenoptera: Halictidae). *J. Kans. Entomol. Soc.* **60**: 100–108.
- Breed, M. D. 1976. The evolution of social behavior in primitively social bees: a multivariate analysis. *Evolution*, **30**: 234–240.
- Cane, J. H. 1983. Chemical evolution and chemosystematics of the Dufour's gland secretions of the lactone-producing bees (Hymenoptera: Colletidae, Halictidae and Oxaeidae). *Evolution*, **37**: 657–674.
- Eickwort, G. C. 1985. The nesting biology of the bee *Halictus farinosus* in California, with notes on *H. ligatus* (Hymenoptera, Halictidae). *Pan-Pac. Entomol.* **61**: 122–137.
- Eickwort, G. C. 1986. First steps into eusociality: the sweat bee *Dialictus lineatulus*. *Fla. Entomol.* **69**: 742–754.
- Eickwort, G. C., and Eickwort, K. R. 1972. Aspects of the biology of Costa Rican halictine bees, II, *Dialictus umbripennis* and adaptations of its caste structure to different climates. *J. Kans. Entomol. Soc.* **44**: 343–373.
- Michener, C. D., and Bennett, F. D. 1977. Geographical variation in nesting biology and social organisation of *Halictus ligatus*. *Univ. Kans. Sci. Bull.* **51**: 233–260.
- Ordway, E. 1965. Caste differentiation in *Augochlorella striata* and *A. persimilis* in eastern Kansas. *Insectes Soc.* **12**: 291–308.
- Packer, L. 1986. The social organisation of *Halictus ligatus* in southern Ontario. *Can. J. Zool.* **64**: 2317–2324.
- Packer, L. 1988. The effect of *Bombylius pulchellus* (Diptera; Bombyliidae) and other mortality factors upon the biology of *Halictus ligatus* (Hymenoptera; Halictidae) in southern Ontario. *Can. J. Zool.* **66**: 611–616.
- Packer, L. 1990. Solitary and eusocial nests in a population of *Augochlorella striata* (Provancher) (Hymenoptera; Halictidae) at the northern edge of its range. *Behav. Ecol. Sociobiol.* **27**: 339–344.
- Packer, L. 1992. Multiple foundress associations in halictine bees. In *Queen number and sociality in insects*. Edited by L. Keller. Oxford University Press, Oxford, U.K. In press.
- Packer, L., and Knerer, G. 1986a. The biology of a subtropical population of *Halictus ligatus* Say (Hymenoptera; Halictidae). I. Phenology and social organisation. *Behav. Ecol. Sociobiol.* **18**: 363–375.
- Packer, L., and Knerer, G. 1986b. An analysis of variation in the nest architecture of *Halictus ligatus* in Ontario. *Insectes Soc.* **33**: 190–204.
- Packer, L., Jessome, V., Lockerbie, C., and Sampson, B. 1989a. The phenology and social biology of four sweat bees in a marginal environment: Cape Breton Island. *Can. J. Zool.* **67**: 2871–2877.
- Packer, L., Sampson, B., Lockerbie, C., and Jessome, V. 1989b. Nest architecture and brood mortality in four species of sweat bee (Hymenoptera; Halictidae) from Cape Breton Island. *Can. J. Zool.* **67**: 2864–2870.
- Sakagami, S. F., and Munakata, M. 1972. Distribution and bionomics of a transpalaeartic halictine bee, *Lasioglossum (Evy-laeus) 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.
- Yanega, D. 1988. Social plasticity and early-diapausing females in a primitively social bee. *Proc. Natl. Acad. Sci.* **85**: 4375–4377.