

Annual variation in survival and reproduction of the primitively eusocial sweat bee *Halictus ligatus* (Hymenoptera: Halictidae)

Miriam H. Richards and Laurence Packer

Abstract: We studied a nesting aggregation of the primitively eusocial sweat bee *Halictus ligatus* near Victoria in southern Ontario during the summers of 1984, 1990, and 1991. Differences in local weather patterns from year to year had marked effects on bee demography and behaviour, belying previous conclusions about "typical" social organization in this aggregation. In 1990, comparatively cool, rainy weather resulted in high nest-failure and low brood-survival rates, while in 1984 and 1991, relatively dry, warm weather had the opposite effect. In 1984 and 1990, spring nest initiation was synchronous and the emergence periods of the first (worker) and second (reproductive) broods were temporally distinct. In 1991, exceedingly warm spring weather caused asynchrony in the timing of nest initiation, accelerated brood and colony development, and continuous brood production. In 1984 and 1990, a few males were produced in the first brood but most were produced in the second brood several weeks later. In 1991, continuous brood production meant that production of males represented the transition between production of workers and of gynes (second-brood females). Patterns of demographic and social variation exhibited by *H. ligatus* at Victoria parallel those observed on a continent-wide geographic scale. This suggests that primitively eusocial sweat bees maintain a variety of reproductive options, adjusting their social behaviour in response to local environmental conditions.

Résumé : Nous avons étudié la contagion des nids chez l'halicte *Halictus ligatus*, une abeille eusociale, près de Victoria, dans le sud de l'Ontario, au cours des étés de 1984, 1990 et 1991. Les différences locales de conditions climatiques d'année en année ont eu un effet décisif sur la démographie et le comportement des abeilles, ce qui vient à l'encontre des conclusions émises par d'autres auteurs sur l'organisation sociale « typique » de la contagion des nids chez cette espèce. En 1990, les taux de succès de la nidification et la survie de la progéniture ont été faibles à la suite de conditions relativement fraîches et pluvieuses. En 1984 et 1991, les conditions relativement sèches et chaudes ont eu l'effet opposé. En 1984 et 1990, toutes les nidifications ont été entreprises en même temps et les périodes d'émergence de la première génération (ouvrières) et de la seconde (reproducteurs) étaient bien séparées dans le temps. En 1991, le printemps a été exceptionnellement chaud, ce qui a eu pour effet de rompre le synchronisme des nidifications, d'accélérer le développement des larves et des colonies et de rendre continue la production de rejetons. En 1984 et 1990, quelques mâles sont issus de la première ponte, mais la plupart des mâles sont issus de la seconde ponte plusieurs semaines plus tard. En 1991, la production continue de nouveaux rejetons a fait que les mâles sont apparus comme une transition entre la production d'ouvrières et la production de nouvelles reines. La variation démographique et sociale observée chez *Halictus ligatus* à Victoria s'apparente à la variation observée à l'échelle de tout le continent. Ces résultats indiquent que les halictes, à organisation sociale primitive, ont toute une gamme d'options reliées à la reproduction et ajustent leur comportement social en fonction des conditions locales du milieu.

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M.H. Richards.¹ Department of Biology, York University, 4700 Keele Street, North York, ON M3J 1P3, Canada, and Department of Biology, University of Utah, Salt Lake City, UT 84112, U.S.A.

L. Packer. Department of Biology, York University, 4700 Keele Street, North York, ON M3J 1P3, Canada.

¹ Present address: Fred Hutchinson Cancer Research Center, 1124 Columbia Street, M-718, Seattle, WA 98104, U.S.A.

Introduction

The growth, development, and activity patterns of insects are strongly affected by environmental conditions, both locally and geographically. In sweat bees (Halictidae), geographic variation in climate is often associated with remarkable flexibility in social behaviour. For instance, in Japan, *LasioGLOSSUM calceatum* (Scop.) is eusocial at low elevations but solitary at high elevations (Sakagami and Munakata 1972), and in the Colorado Rockies, populations of *Halictus*

rubicundus (Christ) exhibit the same pattern (G.C. Eickwort, personal communication). At the northern edge of its range in Nova Scotia, populations of *Augochlorella striata* (Prov.) include solitary as well as eusocial nests (Packer 1990). In northern European populations of *Lasioglossum malachurum* (K.), only a single worker brood is produced each year, but in southern populations two or three worker broods may be produced prior to reproductive-brood females (gynes) and males (Knerer 1987).

Halictus ligatus (Say) is another sweat bee that exhibits marked social variation across its range. It is the most widespread native bee in North America, being found from southern Canada to northern South America, and exhibits geographic variation in both body size and social behaviour (Chandler 1955; Kirkton 1968; Litte 1977; Michener and Bennett 1977; Packer 1986a, 1986b; Packer and Knerer 1986a, 1987). In colder, northern areas, body size is smaller and the colony cycle follows a typical, primitively eusocial pattern in which foundresses raise a brood of workers and then workers help their mother to raise reproductives. Usually there is an extended gap in time between the foundress and worker foraging periods, leading to a distinct age gap between the first and second broods. In temperate colonies, some workers are mated and many show signs of ovarian development, but queens evidently have the greatest individual reproductive rates (Richards et al. 1995). In southern, tropical climates, adult body size is larger, brood production is continuous (i.e., there is no distinct time gap between broods), and although workers are generally produced earlier, worker and gyne production may overlap. Many workers are mated and have developing ovaries, implying a more equitable division of reproduction among the adult females of a nest.

Climate patterns vary temporally as well as geographically, and in temperate regions there may be considerable seasonal and annual variation in climate across the range of a single species (MacArthur 1972). Sweat bee activities, like those of other insects, are strongly affected by daily variation in air temperature and rainfall. Thus, annual variation in summer weather patterns should impinge directly on demographic parameters crucial in determining the nature of social interactions among the occupants of a nest. These parameters might include foraging rates, survival rates of adults or brood, brood productivity, and brood body size. In this paper we investigate the consequences of local environmental variation on the breeding biology of a temperate population of *H. ligatus*. We studied a single nesting aggregation near Victoria in southern Ontario during 3 years in which there were marked differences in weather patterns, especially temperature and rainfall. This year-to-year variation led to demographic changes that affected the nature of colony social organization in ways that reflect the geographic patterns observed in temperate and tropical populations.

Methods

Basic social cycle at Victoria

The basic life cycle of *Halictus ligatus* nesting near Victoria in southern Ontario is summarized here; further details may be found in Packer (1986a, 1986b), Packer and Knerer (1986b), and Richards and Packer (1994). Mated foundresses emerge from their overwintering hibernaculæ in late May or early June and establish nests, usually singly, but occasionally in multifoundress associations. For several weeks, the foundresses forage to provision the first brood, which is composed of small females destined to become workers, and a few males. The second or "reproductive" brood is provisioned by the workers produced in the first brood and is often protandrous. Second-brood females mate, dig overwintering hibernaculæ beneath the natal nest, and enter diapause to become the next generation of foundresses the following spring; they never act as workers. Males do not overwinter. In some nests, one of the workers may become a replacement queen if the original foundress queen dies. Many workers and almost all replacement queens mate and are capable of laying fertilized eggs (Packer 1986a, 1986b; Richards et al. 1995). Although replacement queens are invariably smaller than their mothers, their subsequent social and reproductive behaviour appears to be indistinguishable from that of foundress queens.

Climate data

All climate data were obtained from the Environment Canada meteorological station at Lester B. Pearson International Airport, about 15 km from the field site. *Halictus ligatus* foragers cannot fly when the air temperature is below about 14°C (Richards 1994a). Therefore, to estimate the amount of time during which daytime temperatures were high enough to allow the bees to fly, we calculated the total number of degree-days from base 14°C accumulated from 15 May to 31 August. Mid-May is about the time when hibernating gynes begin to respond to rising soil temperatures. Sweat bees do not forage when it is raining, and developing larvae are susceptible to rotting when the soil remains waterlogged for several days (Packer and Knerer 1986b; Packer 1988), so total rainfall and the number of rainy days per month are both important factors.

Bee data

Extensive nest excavations were conducted from June to September of 1984 (Packer 1986a, 1986b; Packer and Knerer 1986b), 1990, and 1991. To correspond to weather data, excavation dates are reported in terms of the number of weeks from mid-May, beginning with week 1. Nests were excavated after talcum powder was blown down the burrow entrance, making it easier to visualize the burrow. Pupae and larvae that had consumed their entire pollen masses were transferred to small chambers in wax-lined petri dishes and raised to adulthood in the laboratory. Adults were collected in separate microcentrifuge tubes, placed on ice in the field, and later stored at -80°C. Adult females collected in 1984 and 1991 were dissected to determine mating status and the degree of ovarian development. Female caste was determined through a combination of observations of foraging activity of individually marked bees, degree of mandibular wear, whether a female had mated, and degree of ovarian development. Replacement queens were identified as worker-sized individuals with a much higher degree of ovarian development than any of their nestmates; only 1 of 12 discovered in 1984 and 1991 was not mated.

Only single-foundress nests are included in this study. In such nests, the original foundress is invariably larger than the

workers she produces, but in multifoundress nests, subordinate foundresses may be smaller than the workers. Single- and multiple-foundress nests were identified in spring by marking foraging foundresses and by observations of nests. Later in the summer, a few multifoundress nests were identified by very large numbers of brood and by the presence of a foundress smaller than her workers.

Results

Weather

There was considerable variation in the weather among the 3 years 1984, 1990, and 1991. Figure 1 compares total accumulated degree-days after 15 May for each year. Most notably, the summer of 1991 was unusually warm beginning in late May. Figure 2 compares precipitation for June, July, and August, the main brood-rearing months. Particularly critical is the number of rainy days during June and July, when the developing worker brood are most susceptible to rot due to waterlogging. June was particularly rainy in 1990, and July was wet as well. In 1984 and 1991, precipitation in June and July was below average.

Nest development and productivity

Colony development in 1984 and 1990–1991 is compared in Fig. 3. In 1984 and 1990, foraging by foundresses in most nests began within a 3-day period around 4 June and then virtually ceased 2–3 weeks later. Then, with the usual predictability of bee activity at this aggregation, workers began provisioning reproductive brood on 16 July in 1984 and 17 July in 1990 (week 10). In both years the synchrony of first-brood production and the cessation of foraging by foundresses created a noticeable aggregation-wide period of aboveground inactivity before the emergence of adult workers (except in multifoundress nests). In 1991, colony phenology was accelerated relative to 1984 and 1990, and was also less synchronous. A few foundresses began foraging around 21 May, but nest searching and initiation activities by other foundresses were observed for several weeks. Owing to this asynchrony and to apparently accelerated developmental rates, some nests produced first-brood, pigmented pupae as early as week 6 (16–22 June), about 3.5 weeks earlier than expected. Within 1991 nests, a gap in age distinguished the first and second broods, but in the population as a whole, first- and second-brood production was more or less continuous. The overall effect in 1991 was to produce one continuous flight of foundresses and workers, rather than the two separate flights observed in 1984 and 1990.

In 1984 the first brood comprised a mean of 6.65 (SD = 2.6; $n = 20$) individuals per nest (Packer 1986a). Of these, 14.6% were males, so nests produced a mean of 5.65 workers. In 1990, mean first brood size was 5.83 (SD = 3.30; $n = 12$), the proportion of males was 11.5%, and the mean number of workers was about 5.16. In 1991, worker brood size had reached 9.0 individuals per nest (SD = 4.29; $n = 6$) by week 7. At this time males comprised only 5.5% of brood whose sex could be distinguished, so there were already 8.5 juvenile worker brood females per nest. Since no nests were excavated in weeks 8–10, the 1991 estimate of worker number should be regarded as a minimum.

In 1984, first broods were protogynous and second broods

were protandrous (Packer 1986b). The phenology of male and female production in 1990 and 1991 is indicated in Fig. 4. Because of small sample sizes in 1990, frequencies for weeks 11–13 and 16–19 were pooled for the G test of homogeneity. In 1990, brood sex ordering was not detectable ($G = 0.469$, $df = 3$, ns) (but the pattern of investment in males and females was protandrous (Richards 1994a)). In 1991, as in 1984, the second brood was protandrous ($G = 17.61$, $df = 7$, $p = 0.003$), the number of male pupae peaking around week 13 and the number of females about 1 week later, in week 14. In 1991, production of males seems to have represented the transition between production of workers and production of gynes, and in this sense, the first brood could be considered protogynous and the second brood protandrous.

Survival of colonies

The incidence of total nest failure (failure to produce any brood) in 1984, 1990, and 1991 is compared in Table 1. Because slightly different sampling procedures were used in 1984, statistical comparison is limited to 1990 versus 1991. In 1990, only half the nests established in early June survived to produce workers. In all the failed nests, brood loss was mainly due to waterlogging, and most dead brood were rotten. Observations of nests after heavy rainfall, including two whose excavations were interrupted by sudden thunderstorms, indicated that the rain did no harm if followed the next day by drying weather, but caused brood rot if damp weather continued for several days. Feeding larvae were especially susceptible to rot. In 1991, when the weather was warmer and drier, two-thirds of spring nests survived to produce workers. The difference in early nest survival rates in 1990 and 1991 is not quite statistically significant but translates into a significant difference over the entire summer (Table 1).

Nest survival rates following worker emergence in both 1990 and 1991 were considerably higher than during the period preceding worker emergence, and were similar to those in 1984 (Table 1). This demonstrates that the most critical time for nest survival occurs while the foundress queen is the only adult female in the nest.

In September 1991, at least 100 nests near the north end of the nesting area contained gynes preparing for hibernation and were left undisturbed. However, in the spring of 1992, only four foraging foundresses were found. The apparent extinction of this aggregation was likely due to the growth of dense vegetation in the nesting area. Regular herbicide spraying nearby may also have contributed.

Queen and worker survival

Queen survival rates were calculated as the proportion of surviving nests with queens (Fig. 5). In 1984, queen survival began to decline around week 11, 50–70% of foundresses surviving past the peak of gyne pollen ball production around weeks 12 and 13 (Fig. 1 in Packer 1986b). In 1990, foundress survival did not begin to decline until about week 13, a week after peak pollen ball production, and at least 65–75% of foundresses survived to the end of pollen ball production around week 14. In 1991, pollen ball production probably peaked in week 9 or 10 (no nests were excavated at this time, but see Fig. 3). About 75% of foundresses survived past this

Fig. 1. Degree-day accumulation from mid-May during the 5 years in which bees in this study were produced. Note that 1984 and 1990 foundresses were produced in 1983 and 1989, respectively. Degree-days were calculated from base 14°C, the minimum air temperature for sweat bee flight.

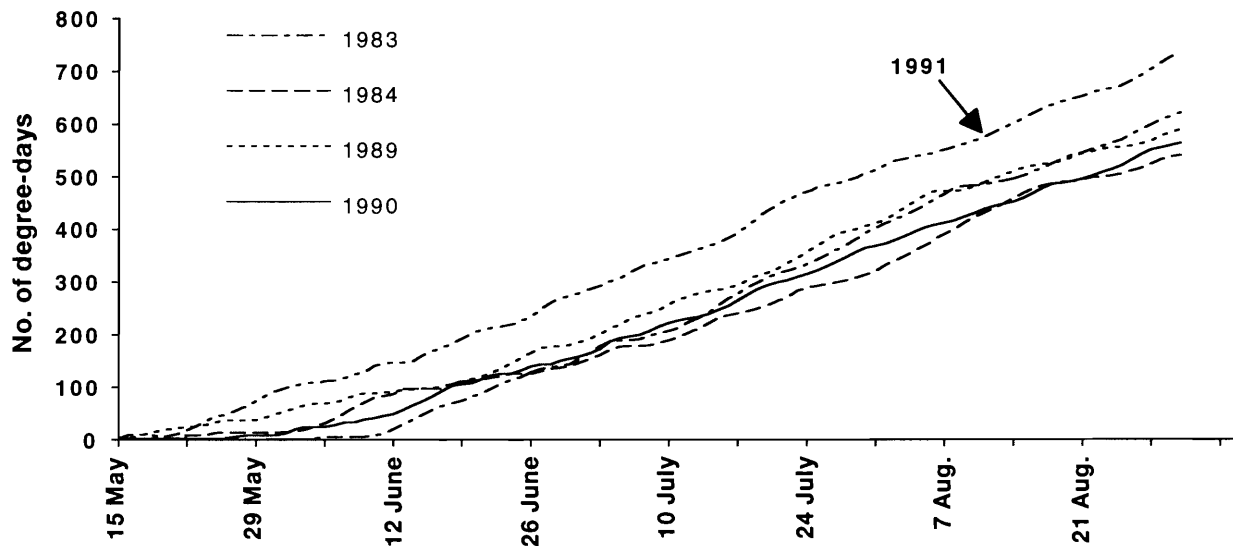


Fig. 2. Annual variation in summer precipitation near Victoria, Ontario, during the 5 years in which bees in this study were produced (see Fig. 1). Means refer to the average rainfall or number of rainy days per month from 1980 to 1992.

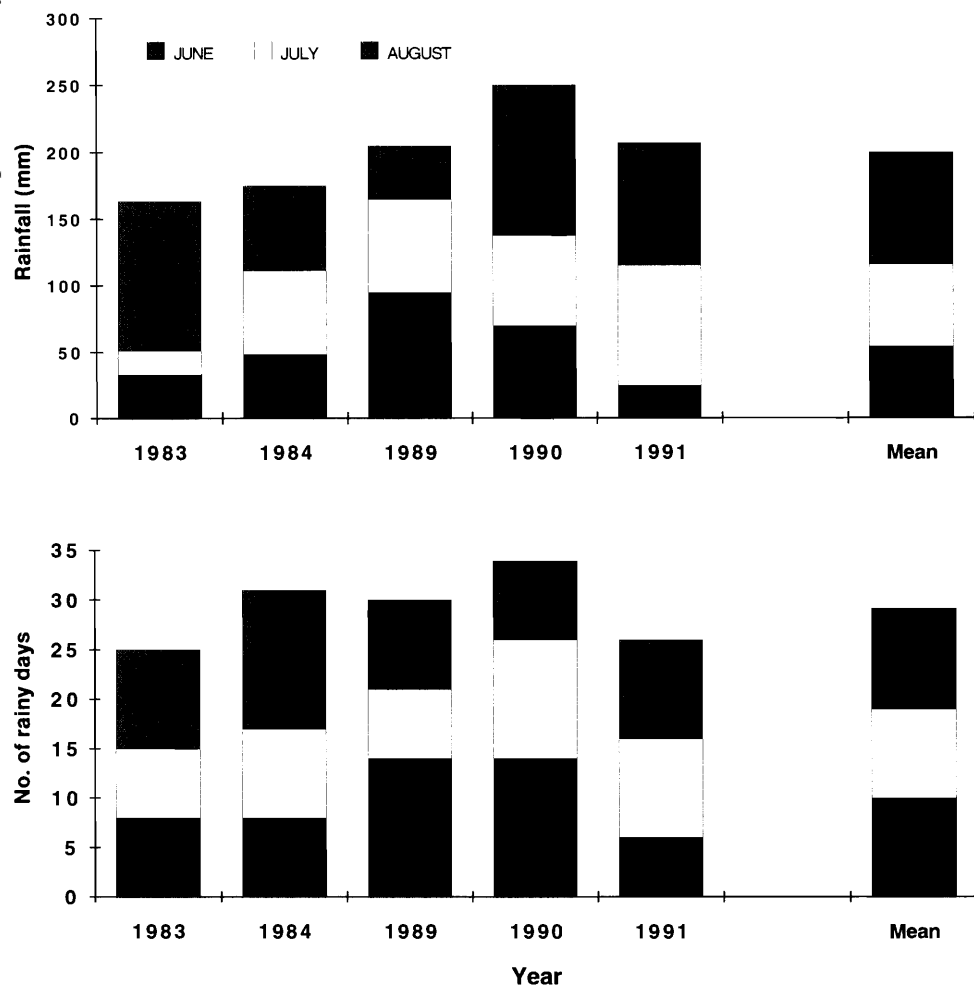
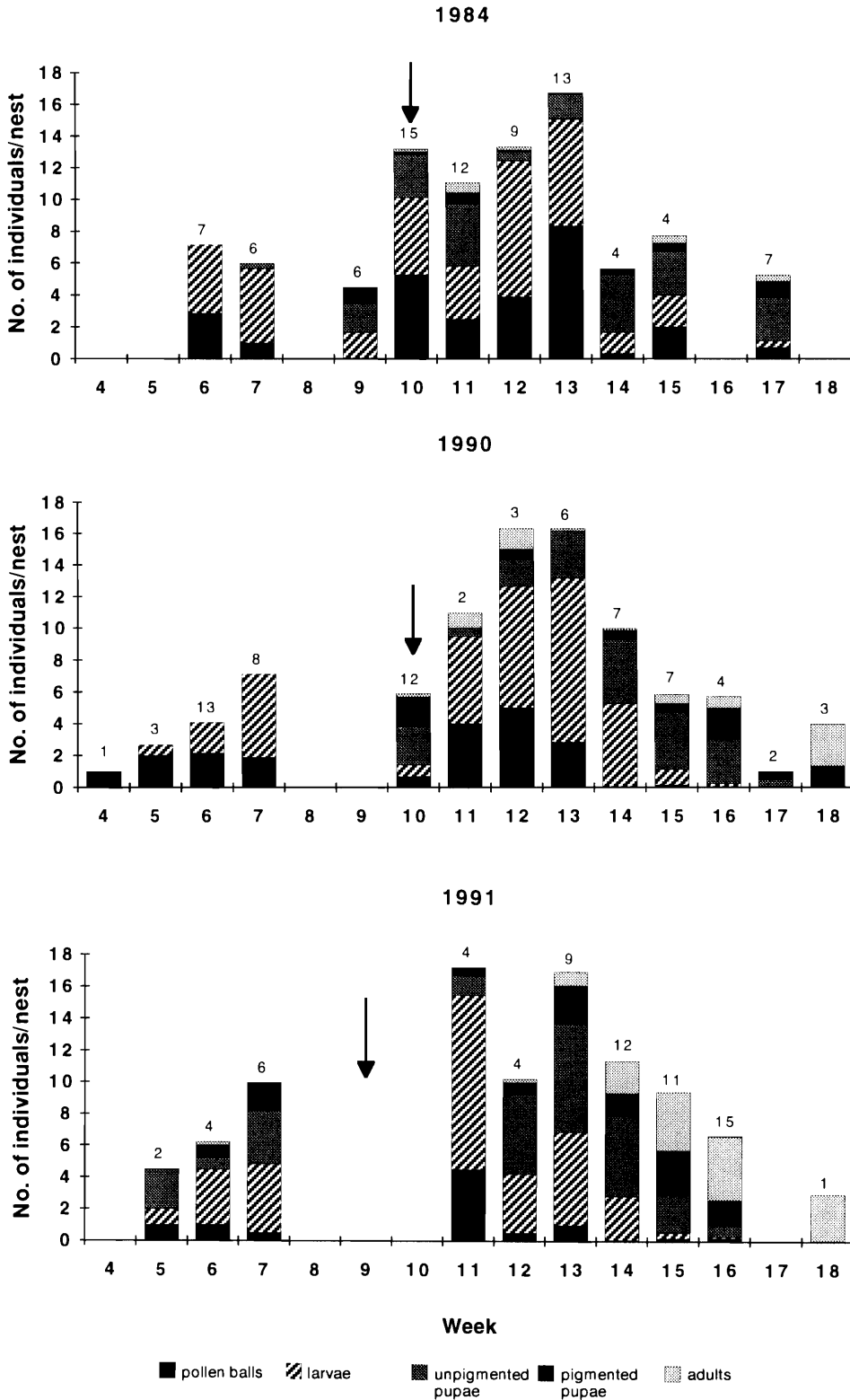


Fig. 3. Brood development in *Halictus ligatus* nests in 1984, 1990, and 1991. The number of nests excavated each week is marked above each bar. Unpigmented pupae are early pupae whose integument has not yet begun to turn black. Pigmented pupae are older pupae in which the pigments are visible. Adults are newly emerged bees found inside their brood cells. The arrows mark the beginning of reproductive brood production in each year. Week 4 is approximately 3–9 June (depending on the year), week 10 is 15–21 July, and week 16 is 26 August – 1 September.



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Fig. 4. Timing of male and female production in 1990 and 1991, based on the number of sexable pupae excavated each week.

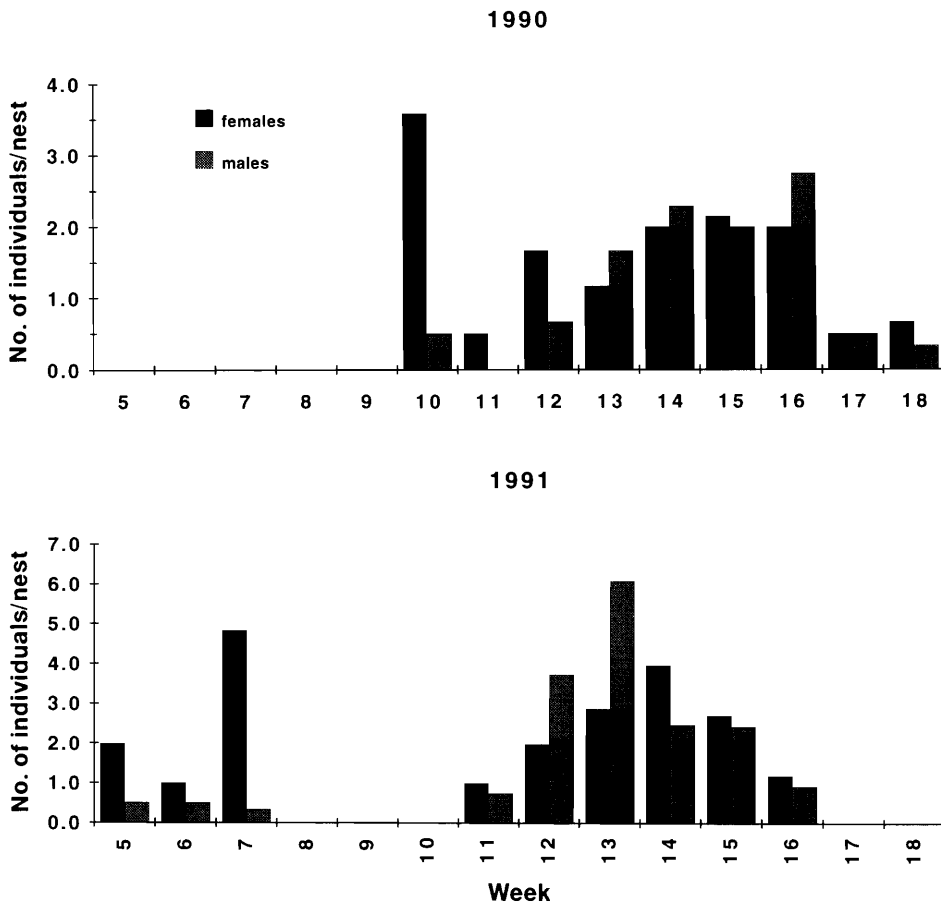


Table 1. Nest survival rates at Victoria, based on the number of nests initiated each spring.

Year	Number of nests			Survival rate (%)		
	Time I	Time II	Time III	Time I–II	Time II–III	Time I–III
1984	130	120	117	92.3	97.5	90.0
1990	49	25	22	51.0	88.0	44.9
1991	78	52	50	66.7	96.1	64.1
<i>G</i> (1990 vs. 1991)				3.06, <i>p</i> < 0.1	1.72, ns	4.52, <i>p</i> < 0.05

Note: Time I is the period of nest initiation by foundresses; time II is the beginning of worker foraging; time III is successful reproductive brood production. Note that the number of nests at time I for 1984 is actually the total number excavated throughout the summer, so 1984 survival rates from time I to II and time I to III may be overestimates. Log-likelihood χ^2 (*G*) tests compare the number of nests with brood dead or alive at the end of an interval in 1990 or 1991 (with 1 degree of freedom).

point, but since survival declined drastically after week 10, this may be an overestimate.

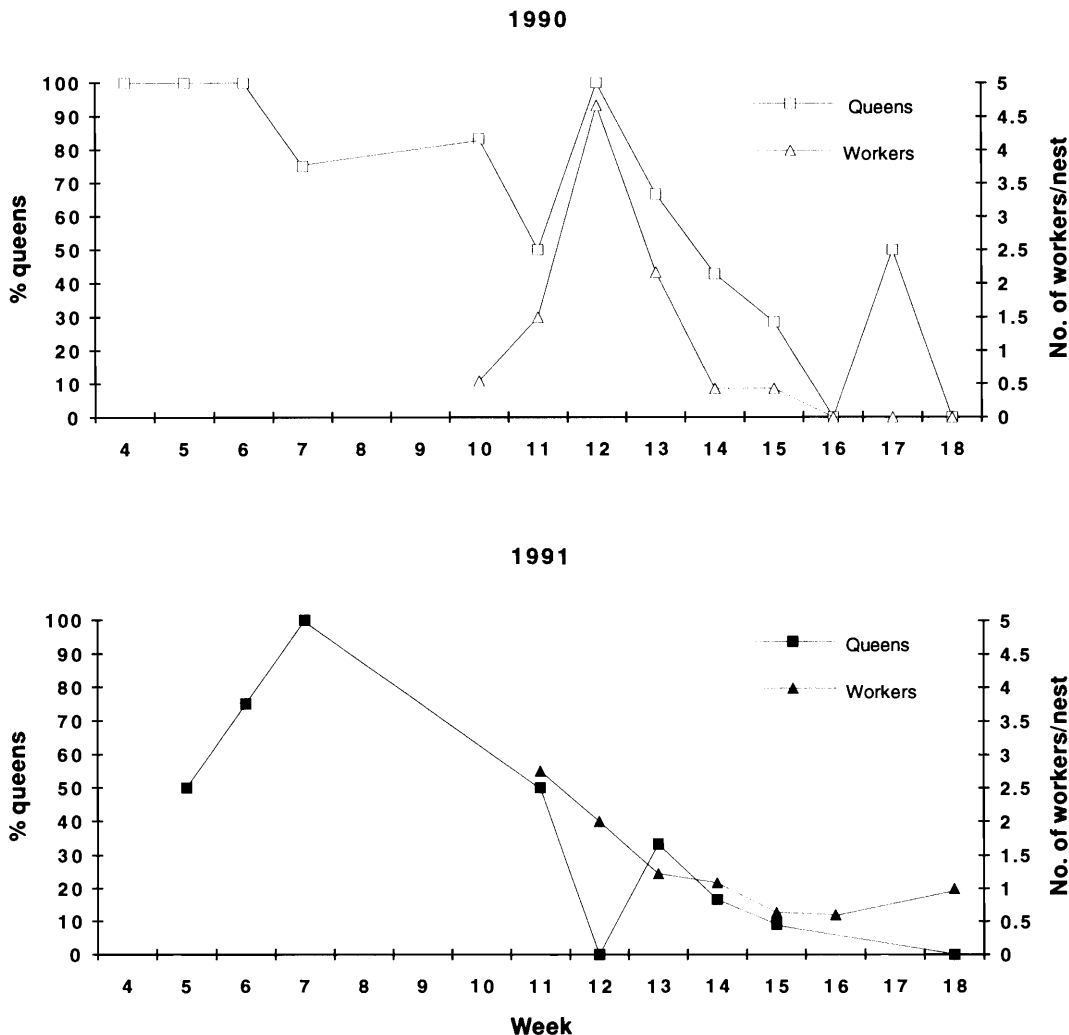
In many nests, almost complete or complete nest failure before the emergence of the worker brood was accompanied by the death of the queen. However, in four nests (two in 1984 and two in 1990), all the brood died but the queen survived. In these nests the queen resumed foraging at the time the workers should have been foraging, and in the 1990 nests this resulted in the successful production of reproductive brood (the 1984 nests were excavated too early to tell).

Replacement queens are workers that become the dominant egg layers following the death of the foundress.

Replacement may be more likely if a queen dies some time after worker emergence (when queens succumb prior to worker emergence, workers sometimes behave as gynes, digging overwintering hibernaculae rather than foraging (Richards and Packer 1994)). In 1984, 9 of 13 queenless nests contained replacement queens and in 1991 the number was 3 of 7.

Worker survival was assessed as the number of workers per nest surviving each week, beginning with the first week of adult worker emergence (Fig. 5). In 1984, nests still contained an average of at least one worker in weeks 15 and 16, and both gyne and male pollen balls were still being pro-

Fig. 5. Queen and worker survival in 1990 and 1991. Queen survival is expressed as the proportion of nests excavated in 1 week that still contained the original foundress. Worker survival is expressed as the number of workers per nest and includes replacement of older workers by younger workers. The apparent jump in queen survival during week 17 of 1990 is based on only two nests.



duced. In 1991, the decline in worker survival after peak pollen ball production coincided with the decline in queen survival. Thus, in late summer of 1984 and 1991, many nests contained actively foraging workers but not the original foundress queen. In 1990, the reverse pattern was observed. That year, very few workers survived past week 13, which is probably why pollen ball production ceased at that time, but until then, almost all nests with active workers also contained a queen. The main cause of worker death was probably predation, especially by phymatid bugs (Richards 1994a), but some workers may have simply worn out (Calabi and Porter 1989); dissections of workers revealed that in some, the tissues were grey and translucent, apparently degrading. Although sample sizes were too small for statistical analysis, there seemed to be more of these later in the summer.

Discussion

The demography and social behaviour of *Halictus ligatus* in Victoria altered significantly in response to capricious spring

and summer weather conditions (see Table 2 for a summary). Variable weather led to variable reproductivity, which in turn led to variation in colony social organization through effects on the caste composition and numbers of females in nests. Especially critical were weather conditions during the production of the worker brood, because they strongly influenced the number of workers per nest, an important determinant of how well queens control worker behaviour and monopolize oviposition (Kukuk and May 1991). *Halictus ligatus* workers do lay eggs when they have the opportunity (Richards et al. 1995). In 1991, when the average number of workers per nest was highest, when workers often outlived queens, and when the degree of queen-worker size dimorphism was relatively small (Richards 1994a), the workers' genetic contribution to the reproductive brood was significantly greater than in 1990, when workers were fewer, relatively smaller (Richards 1994a), and often outlived by the queen. However, failure to monopolize oviposition of the reproductive brood is not necessarily disadvantageous to sweat bee queens. When the number of foraging workers is

Table 2. The influence of weather on the demography and social behaviour of *H. ligatus* in Victoria in 1984, 1990, and 1991.

	1984	1990	1991
Temperature	Warm	Cool	Hot
Rainfall	Below average	Heavy	Moderate
Nest initiation and first-brood emergence	Synchronous	Synchronous	Asynchronous
Nest and brood survival	Good	Poor	Good
No. of first brood	6.65	5.83	≥ 9.0
First-brood sex ratio (% male)	14.6	11.5	5.5
No. of workers	5.65	5.16	8.5
Second-brood sex ratio (% male)	na	50.0	52.0 ^a
Second-brood emergence	Protandrous	Not protandrous	Protandrous
Oviposition pattern ^b	—	Dominated by queens	Large contribution by workers
Colony organization ^b	More eusocial	More eusocial	Less eusocial

^aA clear differentiation between first- and second-brood males was not possible in 1991 (see text).

^bSee Richards et al. (1995).

very large, as it was in 1991, the rate of pollen ball production may outstrip the queen's ability to produce eggs. At Victoria, no female containing more than two fully developed oocytes was ever found, yet the average number of reproductive brood pollen balls per nest was as high as seven or eight (Fig. 3). The queens of such large nests cannot possibly monopolize reproductive brood oviposition, but this loss may be compensated for by gains due to greater overall reproductive brood productivity.

Clearly, annual variation in local weather patterns at Victoria exerted strong effects on sweat bee demography and social interactions within nests. Cooler, wetter weather at Victoria in 1990 also led to the production of brood with smaller body sizes than in 1984 and 1991 (Richards 1994a). Together these trends reflect continentwide variation in *H. ligatus*, which exhibits north-south clines of increasing body size (Kirkton 1968) and apparently increasing productivity by workers (Michener and Bennett 1977). These observations suggest remarkable social lability in this species, such that harsher environmental conditions (temperate climates, Victoria in 1990) promote eusociality, while more beneficent conditions (tropical climates, Victoria in 1991) diminish it. If this is so, then *H. ligatus* exhibits a trend opposite to that of other "socially polymorphic" sweat bees, which sometimes revert to completely solitary behaviour under harsh conditions (Sakagami and Munakata 1972; Packer 1990; Richards 1994b).

Not all the demographic variation observed at Victoria related to females: the numbers and emergence times of males also varied from year to year. The proportion of males in the worker brood is an important determinant of social level (Breed 1976; Packer and Knerer 1985; Yanega 1993), and availability of males undoubtedly affects the reproductive options of first-brood females, since only mated females can produce daughters. In 1984, late production of males in the first brood and protandry of the second brood suggested that first-brood males were destined to mate mainly with second-brood gynes (Packer 1986b). However, in both 1984 and 1990, worker-brood males emerged weeks before the earliest gynes, while in 1991, acceleration of colony development meant that males would have been able to find both workers and gynes to mate with. We suggest that first-brood

males are, in fact, more likely to mate with workers, rarely surviving to mate with gynes (except under unusual conditions, as in 1991). Recent theoretical work (Richards et al. 1995) indicates that the early production of males may be a method for the foundress to exert control on the reproductive brood sex ratio, biasing it towards her own preference before she encounters any resistance from her workers. Yanega (1993) has suggested that in *H. rubicundus*, the availability of males may affect the number of first-brood females that become gynes rather than workers.

For temperate-zone sweat bees, local weather patterns are essentially stochastic series of events that sometimes have drastic effects on parameters which influence social behaviour, including nesting success, brood productivity, and body size (Packer 1990; Yanega 1993). Susceptibility to weather extremes differs among sweat bees with different types of nest architecture. *Halictus ligatus* constructs nests in which the brood cells are small chambers arranged along a main tunnel. In rainy weather, it sometimes constructs small tunnels around the brood cells, which apparently help to keep the soil dry and prevent brood rot (Packer and Knerer 1986b). Evidently this strategy is not always successful, especially in the clay-like soils available to the Victoria aggregation. *Augochlorella striata* constructs clusters of brood cells inside a previously excavated cavity. This type of nest architecture may be less vulnerable to brood rot due to waterlogging, but may be impossible to construct during periods of drought (Packer et al. 1989). In a Cape Breton population of *A. striata*, foundresses ceased foraging during an extended drought period and waited for developing brood to vacate their cells, which were then reused (Packer 1990).

In the face of environmental unpredictability, one successful evolutionary response is bet-hedging (Seger and Brockmann 1987; Philippi and Seger 1988), which could lead to "environmentally organized" variation in social behaviour (W.T. Wcislo, personal communication). Primitively social sweat bees such as *H. ligatus* maintain and exercise a variety of behavioural and reproductive options, pursuing those that are most advantageous at a particular time or place, but opportunities to pursue alternative behavioural strategies may arise only rarely. For example, in *H. ligatus* nests with almost complete worker brood failure accompanied by the death of

the queen, small, first-brood females (workers) may emerge into empty nests. Instead of foraging, these females construct overwintering hibernaculae exactly as if they were gynes (Richards and Packer 1994). The phenomenon of "partial bivoltinism," in which some first-brood females become workers and some become gynes, is likely another example of bet-hedging, since annual variation in the proportion of first-brood females that become foundresses has been observed in several social sweat bees (Sakagami 1977; Yanega 1989; Packer 1990). Bet-hedging strategies that allow flexible reproductive behaviour could eventually result in geographical differentiation of social behaviour as populations adapt to suites of local environmental conditions. The end-result may be facultative sociality, in which individuals, colonies, or populations of social sweat bees express altruistic behaviour to a greater or lesser degree.

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References

- Breed, M.D. 1976. The evolution of social behavior in primitively social bees: a multivariate analysis. *Evolution*, **30**: 234–240.
- Calabi, P., and Porter, S.D. 1989. Worker longevity in the fire ant *Solenopsis invicta*: ergonomic considerations of correlations between temperature, size and metabolic rates. *J. Insect Physiol.* **35**: 643–649.
- Echandler, L. 1955. The ecological life history of *Halictus (H.) ligatus* Say with notes on related species. Ph.D. thesis, Purdue University, Ind.
- Kirkton, R.M. 1968. Biosystematic analysis of variation of *Halictus (Halictus) ligatus* Say (Hymenoptera, Halictidae). Ph.D. thesis, Purdue University, Ind.
- Knerer, G. 1987. Photoperiod as a cue for voltinism and caste regulation in halictine bees. In *Chemistry and biology of social insects*. Edited by J. Eder and H. Rembold. Verlag Johann Peperny, Munich. p. 305.
- Kukuk, P.F., and May, B. 1991. Colony dynamics in a primitively eusocial halictine bee *Lasioglossum (Dialictus) zephyrum* (Hymenoptera: Halictidae). *Insectes Soc.* **38**: 171–189.
- Litte, M. 1977. Aspects of the social biology of the bee *Halictus ligatus* in New York State. *Insectes Soc.* **24**: 9–36.
- MacArthur, R.H. 1972. *Geographical ecology: patterns in the distribution of species*. Harper and Row, New York.
- Michener, C.D., and Bennett, F.D. 1977. Geographical variation in nesting biology and social organization of *Halictus ligatus*. *Univ. Kans. Sci. Bull.* **51**: 233–260.
- Packer, L. 1986a. The social organisation of *Halictus ligatus* (Hymenoptera; Halictidae) in southern Ontario. *Can. J. Zool.* **64**: 2317–2324.
- Packer, L. 1986b. Multiple foundress associations in a temperate population of *Halictus ligatus*. *Can. J. Zool.* **64**: 2325–2332.
- 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., and Knerer, G. 1985. Social evolution and its correlates in bees of the subgenus *Evylaeus* (Hymenoptera; Halictidae). *Behav. Ecol. Sociobiol.* **17**: 143–149.
- Packer, L., and Knerer, G. 1986a. The biology of a subtropical population of *Halictus ligatus* 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., and Knerer, G. 1987. The biology of a subtropical population of *Halictus ligatus* Say (Hymenoptera; Halictidae). III. The transition between annual and continuously brooded colony cycles. *J. Kans. Entomol. Soc.* **60**: 510–516.
- 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.
- Philippi, T., and Seger, J. 1989. Hedging one's evolutionary bets, revisited. *Trends Ecol. Evol.* **4**: 41–44.
- Richards, M.H. 1994a. Social responses to changing environments: reproductive behaviour and reproductive options in a primitively eusocial sweat bee. Ph.D. thesis, York University, North York, Ont.
- Richards, M.H. 1994b. Social evolution in the genus *Halictus*: a phylogenetic approach. *Insectes Soc.* **41**: 315–325.
- Richards, M.H., and Packer, L. 1994. Trophic aspects of caste determination in a primitively eusocial sweat bee. *Behav. Ecol. Sociobiol.* **34**: 385–391.
- Richards, M.H., Packer, L., and Seger, J. 1995. Unexpected patterns of parentage and relatedness in a primitively eusocial bee. *Nature (London)*, **373**: 239–241.
- Sakagami, S.F. 1977. Seasonal change of nest survival and related aspects in an aggregation of *Lasioglossum duplex* (Dalla Torre), a eusocial halictine bee (Hymenoptera: Halictidae). *Res. Popul. Ecol.* **19**: 69–86.
- Sakagami, S.F., and M. Munakata. 1972. Distribution and biometrics of a transpalaeartic eusocial halictine bee, *Lasioglossum (Evylaeus) 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.
- Seger, J., and Brockmann, H.J. 1987. What is bet-hedging? *Oxf. Surv. Evol. Biol.* **4**: 182–211.
- Yanega, D. 1989. Caste determination and differential diapause within the first brood of *Halictus rubicundus* in New York (Hymenoptera: Halictidae). *Behav. Ecol. Sociobiol.* **24**: 97–107.
- Yanega, D. 1993. Environmental influences on male production and social structure in *Halictus rubicundus* (Hymenoptera: Halictidae). *Insectes Soc.* **40**: 169–180.