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## The socioecology of body size variation in the primitively eusocial sweat bee, *Halictus ligatus* (Hymenoptera: Halictidae)

Miriam H. Richards and Laurence Packer

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Patterns of demographic and social variation exhibited by the sweat bee *Halictus ligatus*, reveal that the expression of eusocial colony organization is associated with local environmental conditions, harsher conditions promoting more classical eusociality and gentler conditions promoting diminished eusociality. We examined a variety of factors affecting body size variation of *H. ligatus* at a nesting aggregation near Victoria in southern Ontario, Canada during the summers of 1984, 1990, and 1991. Body size variation was associated with gender and reproductive caste as expected, and there were significant colony effects on size as well. An unexpected result was the dramatic effect of local environmental conditions on body size. Changes in weather patterns from year to year resulted in significant body size variation among all classes of adult sweat bees, including queens, workers, gynes, and males. In 1990 cool, rainy weather led to the production of brood with relatively small body sizes, while in 1984 and 1991, relatively dry, warm weather had the opposite effect. Weather probably influenced brood body size by affecting the ability of adult female bees to gather provisions for the larvae, and so indirectly affecting food availability to brood. Since queens are produced a year before their own workers, environmental factors affecting their relative body sizes are uncorrelated. Nevertheless, the degree of eusocial colony organization is strongly affected by variation in the relative sizes of queens and workers, and this illustrates the extent to which stochastic environmental variation structures opportunities for behavioural interactions in primitively eusocial bees. The pattern of inverse variation between temperature and body size in this bee contradicts the general pattern of increased body size at higher temperatures generally seen in insects and other ectotherms, and indicates that social insects could be an exception to this rule.

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For ectothermic organisms, two major environmental influences on body size are food availability and developmental temperature. In insects, the more food an individual consumes during the larval stages, the larger it is as an adult. This apparently simple relationship is complicated by the effects of temperature. At higher temperatures, insects may develop faster, and so move from one larval stage to the next more quickly, spend less time as feeding juveniles, and end up with smaller

adult body sizes (Ray 1960, Atkinson 1994, Berrigan and Charnov 1994). In species with parental care, adult body size may also be influenced by factors affecting the ability of adults to provision the young. Many insects are mass provisioners, providing a larva with all the food it will consume before developing into an adult. In such species, there exists the opportunity for provisioners to precisely control the size of their offspring in response to ecological factors such as season

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Table 1. The influence of weather on the demography and social behaviour of Victoria *H. ligatus* in 1984, 1990, and 1991 (table slightly modified from Richards and Packer 1995).

	Year		
	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. first brood per nest	6.65	5.83	≥9.0
First brood sex ratio (% male)	14.6	11.5	5.5
No. workers per nest	5.65	5.16	8.5
Second brood emergence	protandrous	not protandrous	protandrous
Oviposition patterns	–	dominated by queens	large contribution by workers
Colony organization	more eusocial	more eusocial	less eusocial

and food availability, and social factors such as the population-wide sex ratio (Wrench and Ebbert 1993). In social insects, body size is also an important corollary of reproductive caste (Breed 1976, Packer and Knerer 1985, Richards and Packer 1994), so environmental influences on body size are inextricably entwined with those affecting demographic and social variation.

A series of recent studies points to the role of environmental variation in organizing the behaviour of primitively social sweat bees (Wcislo in press). In several species, there is marked geographic variation in the expression of eusociality, with populations in harsh climates (e.g. high altitudes) reverting to solitary behaviour (Sakagami and Munakata 1972, Packer 1990, 1991, Richards 1994a, b, Eickwort et al. in press). Variation in social behaviour and colony organization is also observed in sweat bees with less extreme behavioural flexibility. One example is *Halictus ligatus*, a primitively eusocial species that has been studied throughout its geographical range, and in which solitary populations have never been observed. *Halictus ligatus* exhibits strong variation in the degree of eusocial colony organization: harsher environmental conditions promote more classically eusocial behaviour, and gentler conditions lead to diminished eusociality, trends evident at both local and continental scales (Kirkton 1968, Michener and Bennett 1977, Richards and Packer 1995, Richards et al. 1995). By diminished eusociality, we mean that workers' reproductive efforts shift from assisting the queen to raise the queen's reproductive offspring, to raising their own reproductive offspring, including gynes.

Our studies of a population of *H. ligatus* near Toronto in southern Ontario (Table 1; Richards and Packer 1995, Richards et al. 1995) indicate that annual variation in local weather conditions directly influences the demography of sweat bee colonies, and indirectly influences the nature of social interactions among adult females. Under adverse conditions caused by excessive rainfall, sweat bee colonies experienced poor brood

survival, produced few workers, and queens dominated oviposition. Under more favourable conditions due to unusually warm temperatures, colony and brood survival were high, large numbers of workers were produced, and workers laid a large proportion of eggs in the reproductive brood. Such effects may also underlie continent-wide, north-south clines of increasing colony size and decreasing eusociality in *H. ligatus*. In southern areas with long nesting seasons, there are very large numbers of workers per nest, making queen control of worker behaviour less effective than in northern areas with short nesting seasons where there are many fewer workers per nest.

In *H. ligatus* and other primitively eusocial sweat bees, queens control worker behaviour through physical aggression so large numbers of workers make queen control of worker behaviour less effective (Kukuk and May 1991). However, adult body size must also be an important factor governing the outcome of social interactions. *Halictus ligatus* queens have been observed pummelling workers into the sides of nest tunnels or forcing them out the entrance to forage (Packer and Richards unpubl.), and the larger size of the queens clearly confers an advantage in such confrontations. Variation in body size would therefore be expected to contribute substantially to variation in the expression of eusocial behaviour. *Halictus ligatus* exhibits considerable geographic variation in body size (Kirkton 1968), bees from northern populations being generally smaller than bees from southern populations. The cline in body size is very likely related to the north-south clines of increasing colony size and decreasing eusociality, and likewise, could also mirror local patterns of size variation.

In this study, we investigate variation in adult body size and its social and demographic correlates and consequences as part of our overall study of environmentally organized social behaviour of *H. ligatus*. We found that sweat bee body size was strongly influenced by local environmental conditions at Victoria, poor

weather leading to smaller body size and good weather to larger sizes, a pattern that mirrors the continental north-south cline of increasing body size. We also found that the pattern of body size variation was complicated by familial, behavioural and reproductive factors that determine the nature of eusocial interactions in this bee.

## Methods

The life cycle of *H. ligatus* nesting at this aggregation near Victoria in southern Ontario is summarized here; further details may be found in Packer (1986a, b), Packer and Knerer (1986), and Richards and Packer (1995). Extensive nest excavations were conducted at this aggregation from June to September of 1984 (Packer 1986a, b, Packer and Knerer 1986), 1990 and 1991 (Richards and Packer 1995, Richards et al. 1995). Mated foundresses emerge from their overwintering hibernacula to establish nests in late May or early June. Most nests are founded by a single female but there are occasional multifoundress associations. Foundresses forage for several weeks to provision the first brood, which is composed mainly of small females destined to become workers, and a few males. The workers forage and provision the second or reproductive brood, which is composed of males and females technically called gynes. After emergence, the gynes mate, dig overwintering hibernacula beneath the natal nest, and enter diapause preparatory to becoming the next generation of foundresses the following spring.

Climate data were obtained from the Environment Canada meteorological station at Lester B. Pearson International Airport, about 15 km from the field site. Details of summer degree-day accumulation and precipitation for the years 1983–1984 and 1989–1991 may be found in Richards and Packer (1995). Summaries of variation in the weather and previously published patterns of demographic and social variation at Victoria are shown in Table 1.

Only single-foundress nests are included in this study. Depending on the time of excavation, nests contained queens, workers, newly emerged adult brood in their brood cells or in hibernacula (gynes only), pupae, or larvae. Sweat bees are mass provisioners, constructing a mass of pollen and nectar which is the sole source of food for the developing larva. A larva does not pupate until it has consumed its entire pollen mass, so the amount of food supplied directly influences adult body size (but see Richards and Packer 1994). Undamaged pollen masses were collected in separate microcentrifuge tubes and stored in ice. Gyne-producing pollen masses were identified by their large size and peculiar saddle shape (Boomsma and Eickwort 1993, Richards and Packer 1994). Dry weights were obtained by desic-

cation as described in Richards and Packer (1994). Pupae and larvae that had consumed all their food were transferred to small chambers in wax-lined Petri dishes and raised to adulthood in the laboratory. Occasionally, we also attempted to raise medium-sized larvae that had consumed only about half their pollen mass. Invariably, these larvae ceased feeding and almost all of them died, but in a few cases, they successfully pupated, becoming very tiny pupae. Although none of these tiny pupae were included in our size analyses, this shows the direct relationship between amount of food consumed as a larva and final adult body size.

Adult bees collected in the field were placed in separate microcentrifuge tubes on ice. Subsequent storage of all bees was in separate microcentrifuge tubes at  $-80^{\circ}\text{C}$ . Assessment of female caste was based on a combination of body size (workers are invariably smaller than the queens in their own nest), observations of foraging activity by individually marked bees (foundress-queens forage in spring, workers forage in summer, and gynes do not forage), degree of mandibular wear (an indicator of digging activity, engaged in mainly by foundresses and workers), whether or not a female had mated (foundress-queens are always mated but many workers are not), and degree of ovarian development (queens and some workers have highly developed ovaries, but gynes never do). In nests without foundress-queens, replacement queens were identified as worker-sized females with a much higher degree of ovarian development than any of their nestmates.

Head widths (HW) of adults and pupae were measured as the distance across the widest part of the head (including the compound eyes). Wing lengths were measured as the longest linear distance from the point of attachment to the wing tip. Badly damaged wings (i.e. those so severely frayed or torn that the wing tip was gone) or ones that were not fully expanded were not measured. Head measurements were made with a binocular microscope accurate to 0.05 mm and wing measurements with an ocular micrometer accurate to 0.1 mm. In 1990 and 1991 foraging bees were caught, marked, and their head widths measured in the field with the ocular micrometer. Microscope and ocular micrometer measurements agreed to within 0.1 mm and are considered together. The proportional size difference between queens and workers was calculated as

$$(\text{queen HW} - \text{worker HW})/\text{queen HW}$$

## Statistical analyses

We used Model I (Ordinary Least Squares) regression to examine the effects of several variables on size. Model II (Reduced Major Axis) regression is often used for morphometric data, but Model I was justified for several reasons (Sokal and Rohlf 1981): a) causal rather

than associative relationships were examined, b) measurement error was not expected to scale with size and was equal among all classes of individuals, and c) Type II regression is not available for analysis of covariance (ANCOVA) or multiple regression.

We investigated the effects of a variety of independent variables, including size and number of foragers in a nest, year, and nest of origin, on head width variation among queens, workers, gynes, and males. Worker size was the mean size of the workers in a colony and worker number was the number of live workers at the time the colony was excavated. The independent effects of queen and worker size were analysed separately because the two variables were highly correlated (see Results). When more than one bee from the same nest was available (as for workers, gynes, and males), we used nested ANOVA, nesting the variable nest within years. Statistical testing of the Mean Square (MS) for the grouped variable (in this case, year) in an unbalanced nested ANOVA is difficult (Sokal and Rohlf 1981). An approximate significance test is obtained by comparing  $MS_{\text{groups}}/MS_{\text{subgroups}}$ , or in this case,  $MS_{\text{year}}/MS_{\text{nest}}$ .

In order to estimate how much of the variance in adult body size could be ascribed to annual or colony-of-origin (nest) effects, we used nested ANOVA. However, the estimated values should be interpreted with caution since they are based on unbalanced designs.

Whenever *t*-tests were used to compare the mean sizes of two groups, *F*-tests for homogeneity of variances were also done. In all comparisons, the variances were not significantly different ( $p > 0.05$ ).

## Results

The average sizes of foundresses (queens), workers, gynes, and males in nests excavated in 1984, 1990, and 1991 are shown in Table 2. Note that the queens in this sample were produced the year before they were excavated, that is during the summers of 1983, 1989, and 1990. At the simplest level (analysed with one-way ANOVA, Table 2), there are highly significant changes in the average sizes of adult bees from year to year. The sizes of the larval provision masses that produce them may also change from year to year. Gyne-producing pollen masses were significantly larger in 1991 (dry weight mean = 41.3 mg, sd = 2.8,  $n = 13$ ) than in 1990 (mean 34.9, sd = 7.8,  $n = 34$ ;  $t = 2.271$ ,  $df = 45.0$ ,  $p < 0.05$ ). Too few worker and male-producing pollen masses were collected for statistical comparison.

### Queen size

The largest queens were found in 1984 and 1990, while those found in 1991 were significantly smaller (Table 2).

Queens found in 1991 are from the same group of adult females as gynes found in 1990 (see below). In 1984 Packer found that small foundresses (HW < 2.6 mm) were less likely to establish nests successfully and did not survive as long as large foundresses. However, in neither 1990 or 1991, did the average size of foundresses change from early to mid-summer (Table 3A). Moreover, in 1991, foundresses that failed to produce any brood were actually somewhat larger than successful foundresses, although not significantly so (Table 3B). We conclude that there is no unequivocal evidence that foundress head width affects the probability of nest failure.

### Worker size

The largest workers were produced in 1984 by large queens under favourable environmental conditions (Tables 2 and 4). In 1990, small workers were produced by large queens under poor environmental conditions. In 1991, small workers were produced by small queens under favourable environmental conditions. In single-foundress nests, the workers were invariably smaller than the queen that produced them, but the size of workers was strongly correlated with the size of the queen ( $r = 0.49$ ,  $n = 150$ ,  $p < 0.0001$ ). Year-to-year variation accounts for 10.7% of the variance in worker head width, while queen and nest effects together account for 30.2% (nested ANOVA,  $n = 379$ ). We used ANCOVA to partition the effects of variation due to the queen-worker size correlation, further variation as-

Table 2. Average sizes of queens, workers, gynes, and males in 1984, 1990, and 1991. Mean head widths were compared using the Student-Newman-Keuls test ( $\alpha = 0.05$ ) for annual comparisons within a sex or caste. Significant differences among years are indicated by 'S' (small) or 'L' (large).

Sex or caste	Year	Head width mean $\pm$ sd ( <i>n</i> )	Wing length mean $\pm$ sd ( <i>n</i> )
Queens <sup>1</sup>	1984 L	2.92 $\pm$ 0.20 (33)	–
	1990 L	2.96 $\pm$ 0.21 (33)	–
	1991 S	2.74 $\pm$ 0.19 (40)	–
Workers <sup>2</sup>	1984 L	2.58 $\pm$ 0.11 (136)	–
	1990 S	2.53 $\pm$ 0.17 (83)	5.60 $\pm$ 0.29 (12)
	1991 S	2.48 $\pm$ 0.18 (159)	5.43 $\pm$ 0.28 (59)
Gynes <sup>3</sup>	1984 L	2.97 $\pm$ 0.20 (5)	–
	1990 S	2.74 $\pm$ 0.17 (46)	6.06 $\pm$ 0.41 (13)
	1991 L	2.90 $\pm$ 0.18 (213)	6.31 $\pm$ 0.37 (106)
Males <sup>4</sup>	1984 S	2.17 $\pm$ 0.13 (9)	–
	1990 L	2.29 $\pm$ 0.15 (57)	5.76 $\pm$ 0.39 (24)
	1991 L	2.33 $\pm$ 0.16 (184)	5.88 $\pm$ 0.35 (89)

<sup>1</sup> ANOVA:  $F = 13.26$ ,  $df = 2, 103$ ,  $p = 0.0001$ ; SNK:  $MSE = 0.040$ .

<sup>2</sup> ANOVA:  $F = 18.53$ ,  $df = 2, 363$ ,  $p = 0.0001$ ; SNK:  $MSE = 0.023$ .

<sup>3</sup> ANOVA:  $F = 14.31$ ,  $df = 2, 239$ ,  $p = 0.0001$ ; SNK:  $MSE = 0.033$ .

<sup>4</sup> ANOVA:  $F = 4.89$ ,  $df = 2, 229$ ,  $p = 0.0083$ ; SNK:  $MSE = 0.024$ .

Table 3. Two methods of comparing foundress size and nesting success in *H. ligatus*. A. Comparison of head widths of foundresses found in active nests during the period of foraging by foundresses (weeks 5–7) and following the emergence of the first workers (weeks 11–14). Although the mean size increased in both years, the changes were not significant. B. Effect of foundress size on probability of total nest failure (failure to produce any brood at all) in 1991, based on a sample of nests initiated in early spring. Packer (1986a, b) defined females with HW < 2.6 mm as small; here we also use 2.8 mm as a cut-off point. Log-likelihood  $\chi^2$  ( $G$ ) tests compare the frequencies of failed and successful foundresses.

Year	Early nests mean $\pm$ sd ( $n$ )	Mid-summer nests mean $\pm$ sd ( $n$ )	Comparison of means ( $t$ ) and variances ( $F$ )
1990	2.93 $\pm$ 0.19 (22)	3.02 $\pm$ 0.21 (6)	$t = -2.02$ , $df = 26$ , ns $F = 1.12$ , $df = 5, 21$ , ns
1991	2.71 $\pm$ 0.18 (22)	2.79 $\pm$ 0.24 (12)	$t = -1.07$ , $df = 32$ , ns $F = 1.82$ , $df = 11, 21$ , ns

  

Foundress size (mm)	Failed	Successful	Comparison
HW < 2.6	3	5	$G = 0.348$ , $df = 1$ , ns
HW $\geq$ 2.6	8	22	
HW < 2.8	6	15	$G = 0.003$ , $df = 1$ , ns
HW $\geq$ 2.8	5	12	
Mean HW $\pm$ sd	2.76 $\pm$ 0.23	2.72 $\pm$ 0.17	$t = 0.667$ , $df = 36$ , ns

cribable to being raised in a common nest, and environmental variation ascribable to year effects, and found that all these factors contribute significantly to variance in worker head width (Table 4).

Since the annual pattern of worker size variation differed from that observed for queens (Table 2), the proportional size difference between them also changed from year to year (1984: 12.7%, 1990: 15.8%, 1991: 11.4%). Size dimorphism was significantly lower in 1991 than in either 1984 or 1990 (one-way ANOVA:  $F = 3.67$ ,  $df = 2, 18$ ,  $p < 0.05$ ; this statistic is based on a sample in which one queen-worker pair was randomly drawn from each nest with two or more workers in order to avoid biases caused by large nests). The greatest size difference occurred in 1990, the year with the poorest weather conditions, and the smallest difference in 1991, the year with the best weather conditions.

### Gyne size

The largest gynes were produced in 1984 when both queens and workers were also large and weather conditions were favourable. In 1991 weather conditions were also very favourable and gynes produced that year were almost as large as in 1984 despite the fact that queens

Table 4. Analysis of covariance table for factors contributing to variation in worker head width in 1984, 1990, and 1991.

Source	df	MS	$F$	$p$
Model (Y = worker HW)	56	0.057	3.71	0.0001
Queen HW	1	1.168	75.84	0.0001
Year	2	0.117	10.89	0.0001
Nest (year)	53	0.032	2.08	0.0003
Error	207	0.015		

and workers were small. Gynes exhibited the greatest amount of annual variation in size (25.2% of total variance) and a similar amount of inter-nest variation (27.2%, nested ANOVA,  $n = 264$ ). Depending on whether queens or workers determine the sizes of larval provision masses, gyne size variation could result from variation in queen size, worker size, or the number of foragers contributing to a pollen mass (estimated by the number of workers at the time of nest excavation). These possibilities are examined in Table 5. In general, nests with large queens or large workers tend to produce large gynes, but this effect is modified by year.

Table 5. ANCOVA tables for factors contributing to variation in head width of gynes from 1984, 1990, and 1991. Nested analysis of covariance models including the effects of queen or worker head width are considered separately because these two variables are highly correlated. ANCOVA 1: nested model including the effect of queen size, year, and nest effects not attributable to queen HW. ANCOVA 2: nested model including the effect of mean worker size, number of workers per colony, year, and nest effects not attributable to worker HW.

Source	df	MS	$F$	$p$
ANCOVA 1 (Y = gyne HW)	21	0.095	4.70	0.0001
Queen HW	1	0.162	8.03	0.0068
Year	2	0.288	14.26	0.0001
Nest (year) <sup>1</sup>	18	0.070	3.45	0.0003
Error	47	0.020		
ANCOVA 2 (Y = gyne HW)	37	0.107	4.93	0.0001
Mean worker HW	1	0.512	23.63	0.0068
No. workers	1	0.127	5.85 <sup>2</sup>	0.0168
Year	2	0.254	11.71	0.0001
Nest (year) <sup>1</sup>	33	0.085	3.92	0.0001
Error	143	0.085		

<sup>1</sup> Nested variable (pun not intended).

<sup>2</sup> The correlation between gyne head width and worker number is negative.

Table 6. ANCOVA tables for factors contributing to variation in head width of males from 1984, 1990, and 1991. Nested ANCOVA models including the effects of queen or worker head width are considered separately because these two variables are highly correlated. ANCOVA 1: nested model including the effect of queen size, year, and nest effects not attributable to queen HW. ANCOVA 2: nested model including the effect of mean worker size, number of workers per colony, year, and nest effects not attributable to worker HW.

Source	df	MS	F	p
ANCOVA 1 (Y = male HW)	25	0.038	2.12	0.0094
Queen HW	1	0.015	0.83	ns
Year	2	0.034	1.92	ns
Nest (year) <sup>1</sup>	22	0.039	2.20	0.0087
Error	59	0.018		
ANCOVA 2 (Y = male HW)	44	0.043	2.20	0.0004
Mean worker HW	1	0.131	6.76	0.0105
No. workers	1	0.030	6.03	ns
Year	2	0.117	6.03	0.0032
Nest (year) <sup>1</sup>	40	0.037	1.91	0.0036
Error	125	0.019		

<sup>1</sup> Nested variable.

Gyne size was negatively associated with the number of live workers in a nest at the time of excavation.

Foundresses and gynes are members of the same reproductive caste, so comparisons of their sizes are instructive. In 1984, under favourable weather conditions and when foundresses were large, the gynes produced were similar in size to the foundresses ( $t = 0.625$ ,  $df = 37$ , ns). In 1990, when weather conditions were poor but foundresses were again large, the gynes were considerably smaller than the foundresses ( $t = 5.2357$ ,  $df = 77$ ,  $p < 0.0001$ ). These 1990 gynes became the foundresses of 1991. In the warm summer of 1991, the foundresses produced gynes significantly larger than themselves ( $t = 5.08$ ,  $df = 251$ ,  $p < 0.0001$ ). The size of gynes did not seem to be associated with overwintering success: 1990 gynes did not differ in size from the 1991 generation of foundresses (means:  $t = 0.078$ ,  $df = 84$ , ns; variance:  $F = 1.15$ ,  $df = 39,45$ , ns).

## Male size

In males, annual effects accounted for only 7.4% of the variation in head width with 20.7% originating in differences between nests (nested ANOVA,  $n = 250$ ), an amount smaller than seen in any group of females (Table 2). In fact, the annual effect may be illusory, a statistical effect of the small 1984 sample ( $n = 9$ , but compare ANCOVAs 1 and 2, Table 6). Male size was not correlated with queen size or worker number but was significantly associated with worker size (Table 6).

## Discussion

In this paper we report significant variation in body size in all four classes of adult *Halictus ligatus* in southern

Ontario. Ecological factors affecting both body size and the degree of queen-worker size dimorphism include temperature, rainfall, and food availability. The latter also counts as a social factor affecting body size, because both caste and gender influence the total amount of food with which any particular larva will be provided. Another social factor is the tendency for size to be correlated among nestmates. These results are important for several reasons. First, they illustrate that there can be a large amount of environmentally based variation in body size, even in an insect with parental care in which juveniles do not have to forage for themselves. Second, they illustrate the major role environmental factors play in structuring opportunities for social interaction in insects. Third, they contrast with results from diverse ectotherms, including insects, showing that cold temperatures result in maturation later and at a larger size compared to development at higher temperatures. We discuss these issues below, emphasizing the role of the environment in determining phenotypic variation in size and the consequences of this variation for conflicts between queens and workers and among workers over reproductive opportunities in the nest.

Annual variation in body size of *H. ligatus* nesting at Victoria mirrored the patterns of demographic and social variation observed among the bees at this site (Richards and Packer 1995, Richards et al. 1995). In 1984, when both temperatures and rainfall were moderate and average, bees experienced relatively high nest and brood survival, brood body sizes were generally large, and the degree of queen-worker size dimorphism was intermediate. In 1990, when excessive rainfall and cool temperatures resulted in poor nest and brood survival, brood body size was generally small, the degree of queen-worker size dimorphism was high, and queens dominated oviposition of the reproductive brood. In 1991, when unusually warm temperatures and moderate rainfall combined to produce good nest and brood survival, large brood body size, and low queen-worker size dimorphism, workers significantly increased their share of reproductive brood oviposition. Clearly, local environmental variation is an important extrinsic organizer (Wcislo in press) of colony social interactions mediated by changes in body size and demography.

The strong effects of local weather variation on *H. ligatus* body size were not unexpected: the pattern at Victoria paralleled the known north-south cline of increasing body size across North America (Kirkton 1968). In insects generally, adult body size is a function of the quantity and quality of food consumed during the larval stages. The dramatic effect of food quantity on body size in *H. ligatus* is observed in half-grown larvae that cease feeding in the laboratory and metamorphose into tiny pupae about half the size of normal pupae. However, the effect of food quantity and quality is complicated by the effects of larval developmental temperatures. At higher temperatures, insects generally

develop faster (i.e. they change from one larval stage to the next more quickly) and spend less time as feeding juveniles, thus producing smaller body sizes at higher temperatures (Ray 1960, Atkinson 1994, Berrigan and Charnov 1994). This is the opposite of the patterns observed in *H. ligatus* at Victoria or across North America. Can these observations be reconciled?

We have no information about the physiological efficiencies or metabolic rates of juvenile *H. ligatus*, but higher temperatures apparently increase developmental rates: in 1991, unusually warm temperatures led to the appearance of worker brood pupae about 3.5 weeks earlier than expected (Richards and Packer 1995). In the Victoria aggregation, brood develop underground at depths of about 5–25 cm (Packer and Knerer 1986), earlier brood generally being closer to the surface than later brood. While being underground would undoubtedly have mitigated variation in temperature, this would have been less so for the worker brood than for the reproductive brood since worker brood cells were closer to the soil surface. So it seems that developmental temperature per se did have the expected effect on *H. ligatus*, that is to increase developmental rate. In most insects, the larvae are independent and must forage for themselves, and would have less time to do so if higher temperatures cause them to reach the stage of metamorphosis more quickly. In mass provisioners such as sweat bees, the larvae are supplied with a predetermined amount of food before the egg is even laid. Since they always consume the entire food mass before pupation, developmental temperatures do not affect the amount of food they consume. In fact, the amount of food consumed is influenced by weather conditions affecting foraging females. Thus insects that mass-provision their brood, and possibly others that exhibit parental care, may be exceptions to the general rule that higher temperatures lead to decreased body size in insects, because juveniles do not have to find their own food.

The influence of weather on *H. ligatus* body size was probably determined by direct effects on foraging and brood provisioning by adult females. The influences of summer temperatures and weather are confounded, since in southern Ontario, rainy weather is often associated with lower temperatures and sunny weather with higher temperatures. Sweat bees do not forage during rainy weather and at Victoria, *H. ligatus* were incapable of flying when air temperatures dropped below 14°C (Richards 1994a), but above this threshold, lower air temperatures probably did not interfere with sweat bee foraging activity. Female bees are able to exert precise control over the amount of pollen and nectar in larval provision masses, which show consistent differences in size and shape, depending on whether they will produce workers, gynes or males (Boomsma and Eickwort 1993, Richards and Packer 1994). Since the pollen and nectar for a single provision mass are collected in one day (Richards and Packer unpubl.), we suspect that when

poor weather constrains foraging time, less pollen and nectar are gathered and fewer, smaller bees are produced. Apparently this is what happened during the excessively rainy summer of 1990, when a generation of large-sized foundresses produced workers, and then gynes, that were very small in size. The rain also caused high rates of worker brood mortality (Richards and Packer 1995). The small gynes of 1990 became the small queens of 1991, but unusually warm and relatively dry weather allowed them to produce many, comparatively large-sized workers, and eventually, large-sized gynes as well. A similar negative effect of poor weather on body size has been observed in a population of *Lasioglossum cinctipes* nesting in a marginal environment in Nova Scotia (Packer et al. 1989). Interestingly, Kamm (1974) found that lower temperatures led workers of a laboratory population of *Lasioglossum zephyrum* to construct larger brood cells with larger provision masses, but these bees would have been sheltered from severe weather such as rain.

The year-to-year pattern of size variation in males was slightly different from that observed in females, the smallest males being found in 1984 when the largest workers and gynes were produced. The lower variance of male size may indicate as yet undiscovered size constraints on males, especially if male body size is positively correlated with sperm production (Berrigan and Locke 1991) or if it affects sustained flight efficiency. Alternatively, the sizes of males may have more to do with sex allocation decisions made by the queen (Richards et al. 1995). Patterns of sex allocation are predicted to change in response to the same environmental influences that affect worker productivity and may reflect the efforts of the queen to bias the reproductive brood sex ratio toward males in the period before she loses control to the workers (Richards et al. 1995).

At Victoria, *H. ligatus* from the same nest tended to be similar in size. Foundresses construct the pollen masses that produce workers and first-brood males, while workers forage for and probably also construct reproductive brood provision masses. It is not clear whether the queens or the workers are the final arbiters of pollen ball size. This is important because correlations between the sizes of foragers and brood could result either from genetic correlation of parents and offspring or simply represent a scaling effect resulting from foragers using their own bodies as a basis for measuring the sizes of the provision masses. It would be difficult to distinguish between these two causes of correlation except in a laboratory experiment in which the sizes of provision masses could be artificially manipulated (Thomas 1993). The fact that male body size correlates with worker size but not queen size may indicate that workers make the decisions about the sizes of reproductive brood pollen masses, although it is likely that queens control decisions about the sex of the brood (Richards et al. 1995). In any case, there is a

strong tendency for large *H. ligatus* queens to produce large workers that in turn produce large gynes and males (with fewer data, Packer and Knerer [1986] reached a different conclusion, because they found no correlation between forager size and brood cell volume, which is correlated with brood head width [Kumar 1975]).

Frank and Crespi (1989) have suggested that when there are more workers in a nest, they cooperatively produce larger gynes. If this were true, it would suggest that larger numbers of workers in 1991 would explain larger gyne body sizes that year. However, after correcting for size similarity among nestmates, we actually found an inverse relationship between worker number and gyne size, and Packer and Knerer (1986) found no correlation between worker number and the volume of gyne brood cells. Frank and Crespi's hypothesis depends on the additional assumption that reproductive brood oviposition is monopolized by queens, a situation which did not occur at Victoria in 1991. Many gynes were the daughters, rather than the sisters, of the workers that produced them, so the workers in a large nest would have been cooperating to provision a brood of daughters, sisters, and nieces. Furthermore, it appears that in some colonies with large numbers of workers, they interfere with each other or that some workers are more inclined to be "lazy" (Eshel and Motro 1988, Richards unpubl.). Finally, it is possible that our estimate of worker number is not accurate since we used the number of workers alive when a nest was excavated, rather than the actual number of workers provisioning particular brood.

We had expected to find that in female sweat bees, specifically foundresses, large body size would be associated with enhanced survival or reproductivity (Honek 1993). We found no evidence for this prediction, although the selective effects of body size could be more subtle than detectable from our data. Similar results have been found in studies of the blue orchard bee *Osmia lignaria* (Tepedino and Torchio 1989). Perhaps there is no selective advantage of large body size in females, except as it relates to social aspects of caste (overall body size might be determined by inter- rather than intraspecific competition [J. Seger pers. comm.]). Since there is broad overlap in the size distributions of queens and workers (Packer 1986a, b, Richards and Packer 1994), body size per se does not determine a female's reproductive or social status. Relatively small females are more susceptible to manipulation by large females (Kukuk and May 1991), but reproductive opportunities are also affected by females' physiological condition and the social milieu of the nest (Richards and Packer 1994). In short, large *H. ligatus* females often, but not always, become foundresses, which often but not always, monopolize oviposition at the expense of subordinate foundresses (Packer 1986b) and workers (Richards et al. 1995). In laboratory colonies of *La-*

*sioglossum zephyrum*, large bees also tend to be dominant to smaller bees, and large workers are more likely to lay eggs than small workers, apparently because the queens find small workers easier to control (Kukuk and May 1991). All these observations support the contention that the degree of size dimorphism between queens and workers or subordinates is an important determinant of the strength of eusocial colony organization (Breed 1976, Packer and Knerer 1985).

Year-to-year variation in the degree of queen-worker size dimorphism is essentially stochastic, because queens and workers are produced in different years, and environmental conditions affecting their sizes are uncorrelated. Why don't queens simply make workers that are sufficiently smaller than themselves to dominate easily? If worker size is associated with ergonomic efficiency, predation risk, longevity, or success as a replacement queen, then there may be a minimum worker size below which there is a negative impact on the nest's second brood productivity. Even in nests with viable queens, workers may still produce substantial portions of the reproductive brood when the rate at which larval provisions are collected outstrips the queen's egg-laying ability (Richards and Packer 1995). It may be more of a disadvantage for small queens to make workers so small that they can easily be controlled, than to allow them a share of reproductive brood oviposition.

For temperate sweat bees, local weather patterns are unpredictable, especially over the course of an entire summer or from year to year, but they have drastic effects on nesting success, brood productivity, and body size, all of which impinge directly on colony social organization. In the face of such unpredictability, *Halictus ligatus* has maintained a high degree of behavioural flexibility in which the expression of eusocial behaviour is continuously adjusted in response to the harshness of local environmental conditions. Under poor conditions and at higher latitudes, eusocial behaviour is more strongly expressed than under favourable conditions or at lower latitudes.

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## References

- Atkinson, D. 1994. Temperature and organism size – a biological law for ectotherms? – *Adv. Ecol. Res.* 25: 1–58.  
Berrigan, D. and Locke, S. J. 1991. Body size and male reproductive performance in the flesh fly, *Neobellieria bulata*. – *J. Insect Physiol.* 37: 575–581.

- and Charnov, E. L. 1994. Reaction norms for age and size at maturity in response to temperature: a puzzle for life historians. – *Oikos* 70: 474–478.
- Boomsma, J. J. and Eickwort, G. C. 1993. Colony structure, provisioning and sex allocation in the sweat bee *Halictus ligatus* (Hymenoptera: Halictidae). – *Biol. J. Linn. Soc.* 48: 355–377.
- Breed, M. D. 1976. The evolution of social behavior in primitively social bees: A multivariate analysis. – *Evolution* 30: 234–240.
- Eickwort, G. C., Eickwort, J. M., Gordon, J. and Eickwort, M. A. In press. Solitary behavior in a high-altitude population of the social sweat bee *Halictus rubicundus* (Hymenoptera: Halictidae). – In: Crespi, B. and Choe, J. C. (eds), Social competition and cooperation in insects and arachnids: II. Evolution of Sociality. Princeton Univ. Press, Princeton, NJ.
- Eshel, I. and Motro, U. 1988. The three brothers' problem: kin selection with more than one potential helper. 1. The case of immediate help. – *Am. Nat.* 132: 550–566.
- Frank, S. A. and Crespi, B. J. 1989. Synergism between sib-rearing and sex ratio in Hymenoptera. – *Behav. Ecol. Sociobiol.* 24: 155–162.
- Honek, A. 1993. Intraspecific variation in body size and fecundity in insects: a general relationship. – *Oikos* 66: 483–492.
- Kamm, D. R. 1974. Effects of temperature, day length, and number of adults on the sizes of cells and offspring in a primitively social bee (Hymenoptera: Halictidae). – *J. Kans. Entomol. Soc.* 47: 8–18.
- Kirkton, R. M. 1968. Biosystematic analysis of variation of *Halictus (Halictus) ligatus* Say (Hymenoptera, Halictidae). – PhD thesis, Purdue Univ., Michigan.
- 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.
- Kumar, S. 1975. Relations among bee size, cell size, and caste, in *Lasioglossum zephyrum* (Hymenoptera, Halictidae). – *J. Kans. Entomol. Soc.* 48: 374–380.
- 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.
- 1986b. Multiple foundress associations in a temperate population of *Halictus ligatus*. – *Can. J. Zool.* 64: 2325–2332.
- 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.
- 1991. The evolution of social behavior and nest architecture in sweat bees of the subgenus *Evylaeus* (Hymenoptera; Halictidae): a phylogenetic approach. – *Behav. Ecol. Sociobiol.* 29: 153–160.
- and Knerer, G. 1985. Social evolution and its correlates in bees of the subgenus *Evylaeus* (Hymenoptera; Halictidae). – *Behav. Ecol. Sociobiol.* 17: 143–149.
- and Knerer, G. 1986. An analysis of variation in the nest architecture of *Halictus ligatus* in Ontario. – *Insectes Soc.* 33: 190–204.
- , Jessome, V., Lockerbie, C. and Sampson, B. 1989. The phenology and social biology of four sweat bees in a marginal environment: Cape Breton Island. – *Can. J. Zool.* 67: 2871–2877.
- Ray, C. 1960. The application of Bergmann's and Allen's rules to the poikilotherms. – *J. Morphol.* 106: 85–108.
- Richards, M. H. 1994a. Social responses to changing environments: Reproductive behaviour and reproductive options in a primitively eusocial sweat bee. – PhD thesis, York Univ., North York, Ontario.
- 1994b. Social evolution in the genus *Halictus*: A phylogenetic approach. – *Insectes Soc.* 41: 315–325.
- and Packer, L. 1994. Trophic aspects of caste determination in a primitively eusocial sweat bee. – *Behav. Ecol. Sociobiol.* 34: 385–391.
- and Packer, L. 1995. Annual variation in survival and reproduction of the primitively eusocial sweat bee, *Halictus ligatus* (Hymenoptera: Halictidae). – *Can. J. Zool.* 73: 933–941.
- , Packer, L. and Seger, J. 1995. Unexpected patterns of parentage and relatedness in a primitively eusocial bee. – *Nature* 373: 239–241.
- Sakagami, S. F. and Munakata, M. 1972. Distribution and bionomics 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.
- Sokal, R. R. and Rohlf, F. J. 1981. *Biometry*, 2nd ed. – Freeman, New York.
- Tepedino, V. J. and Torchio, P. F. 1989. Influence of nest hole selection on sex ratio and progeny size in *Osmia lignaria propinqua* (Hymenoptera: Megachilidae). – *Ann. Entomol. Soc. Am.* 82: 355–360.
- Thomas, R. H. 1993. Ecology of body size in *Drosophila buzzatii*: untangling the effects of temperature and nutrition. – *Ecol. Entomol.* 18: 84–90.
- Wcislo, W. T. In press. Behavioral environments of sweat bees (Halictinae) in relation to variability in social organization. – In: Crespi, B. and Choe, J. C. (eds), Social competition and cooperation in insects and arachnids: II. Evolution of Sociality. Princeton Univ. Press, Princeton, NJ.
- Wrench, D. L. and Ebbert, M. A. 1993. Evolution and diversity of sex ratio in insects and mites. – Chapman and Hall, New York.