

Social plasticity and early-diapausing females in a primitively social bee

(Halictidae/*Halictus*/polyethism/caste determination/partial bivoltinism)

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ABSTRACT Many of the females of the first summer brood of the sweat bee *Halictus rubicundus* mate, soon vanish from the nesting site, undergo diapause, and return unworn the following spring to found their own nests without ever functioning as workers. Roughly half a season's foundresses may originate in this way. This finding contradicts previous assumptions regarding timing of reproductive production in sweat bees and offers a remarkable example of intraspecific social diversity; some females in the population behave as solitary bees while others are social. Such behavior may be widespread in bees and wasps, for it is almost undetectable with ordinary field techniques. These findings require the reevaluation of previous studies of sweat bee life cycles and of theories and models of the evolution of primitive insect societies.

The behavioral evolution of the social Hymenoptera is often viewed as a hypothetical continuum of species from solitary to social (1), and studies of primitively social bees and wasps have typically been interpreted in this context. However, some recent investigations have emphasized intraspecific variation in social behavior: single populations containing individuals whose behavior ranges from solitary to eusocial (2–5). Such behavioral diversity suggests that environmental factors play a large role in the expression of social behavior (C. D. Michener, personal communication). For many species, sociality may be facultative rather than obligate, permitting assessment of the immediate ecological pressures favoring or inhibiting sociality. Such species may reveal some of the ultimate origins of sociality and the behavioral mechanisms involved.

The Halictidae contains both solitary and primitively eusocial species. Where castes exist, they are not believed to be genetically specified. Temperate primitively eusocial species are typically thought to have life cycles in which mated females emerge from diapause in the spring, excavate nests in the ground, and rear a first brood consisting of workers and commonly a few males. The workers remain in their mothers' nests and help rear a second (sometimes prolonged) brood consisting of males and young future foundresses; the latter mate, enter diapause, and restart the cycle the following spring. Thus, there is ordinarily one generation, but two (sometimes more) broods of offspring. If a queen dies in midseason, however, one of her daughters commonly becomes a replacement queen; first-brood males supposedly are produced in order to mate with such females. Offspring of replacement queens or workers represent a partial second generation, so that the population is partially bivoltine.

High "mortality" (or "rapid turnover") among first-brood halictid females, the so-called workers, is commonly observed and often not published. In the present study, however, mark-recapture techniques showed that disappearing

"workers" of *Halictus rubicundus* are often future nest foundresses (gynes) that rapidly leave the population to enter diapause until the following spring without ever acting as workers. Thus, reproductives are produced all season long, and within the population some females function as solitary bees, while others may form eusocial colonies. The simultaneous production of workers and gynes violates some basic assumptions in theories of halictid caste determination and social evolution (6–8), necessitating a reappraisal of halictid evolutionary theory.

MATERIALS AND METHODS

H. rubicundus is considered a typical primitively eusocial halictine, although only sketchy details of its biology have been described (9–12). I individually marked, measured, and observed the activities of this species (*ca.* 700 bees per year) for six consecutive seasonal cycles, 1982–1987, in an aggregation that typically contained from 50 to 120 nests. The aggregation (in the borough of Queens, New York City) was observed for a total of >2500 hr on virtually every day that the bees were active, with the following exceptions: the early nest-founding phase in 1982 and the termination of the second-brood emergence in 1983, 1984, 1986, and 1987. Observations were continuous (weather permitting) from between 0830 and 1030, when flight activity began, until 1500–1700, when activity ceased. Bees were given individualized enamel paint markings color-coded by week, and the right forewing (including tegula) was measured to the nearest 0.1 mm. The markings permitted compilation of complete life histories from the date of first emergence from the natal nest for virtually every bee in the population.

The aggregation was naturally divided into eastern and western nest clusters, the former being initially larger and therefore the primary study site. In the 5 years that I have observed returning marked foundresses in the eastern nest cluster, most returned within 0.5 m of their natal nest, and only 4 bees (of >220) moved to the western cluster (the clusters' nearest nests are some 3 m apart). This strong philopatry suggests that year-to-year population statistics remain largely "uncontaminated" by immigration from other sites or by switching between nest clusters.

RESULTS

Seasonal Cycle. The seasonal cycle of the population, generalized from all observations, was as follows: Foundresses returned to the study site from unknown overwintering locations in late April to excavate new nests. Despite initial bouts of usurpation and nest-switching, all nests were monogynous. Foundresses excavated and provisioned their nest cells with pollen and nectar for roughly 1 month and then remained inactive for about 2 weeks (thus creating a gap between brood production periods) until the first brood (the "worker" brood of comparable halictid studies) began to emerge in mid-to-late June.

This brood, emerging over a 1-month period, was slightly protogynous and consisted of about five to eight offspring per nest (up to 15), some 25% of which are males (1982, 17.7%; 1983, 17.8%; 1984, 18.4%; 1985, 30.6%; 1986, 31.9%; and 1987, 32.4%). Up to eight or nine daughters (typically three or four) would remain and function as workers while the foundress remained underground as colony queen. Emerging bees averaged larger as the emergence progressed; workers were primarily among the smaller, earlier emerging females, as were the females that replaced missing foundresses (replacement queens).

As the emergence progressed, increasing numbers of emerging females disappeared (mostly to enter diapause—e.g., 43% of the total in 1984; Fig. 1). Thus, a mixture of social and “nonsocial” females was produced in many nests; one or more females remained to form eusocial (mother and daughters) or parasocial (all sisters) colonies, while most or all of the later-emerging females left the nest without ever having acted as workers. Within any given nest, gynes often (66% of cases in 1984) emerged after worker production had ceased. Some nests were abandoned entirely by the emerging bees, particularly where brood size was small, and the bees thereby exhibited a “solitary” life cycle. The average size of departing females was significantly larger than that of workers, but this appears to be a result of their late emergence date, rather than being causally related to their behavior (unpublished data). Cell construction and provisioning by the workers often stopped by the time the first emergence period ended, followed thereafter by at least 1 week of inactivity before the second brood began to emerge in late July.

The second brood (the “reproductive” brood) was protandrous, was composed roughly of 60% males, and contained fewer total bees than the first brood. Emerging females all left the area to enter diapause after mating. The workers and queens died, so that by the end of August, few, if any, bees remained in the nesting site.

Early-Diapausing Females. The following phenomena elucidate the nature of diapausing first-brood females.

(i) No foundress was ever known to function as a worker; fewer than 6 of >100 were recorded as carrying any pollen prior to diapausing (the cumulative amount was not even sufficient for half a pollen mass), and the remainder never gathered pollen.

(ii) Future foundresses of the first brood disappeared within the first few days after emergence from their nests [for 1985 foundresses, the median stay was 3 days (range = 1–9, $n = 41$; two females in otherwise vacant nests remained 16 days)]. Without the markings and follow-up observations, these bees would have been considered workers that died before beginning to collect pollen.

(iii) No foundress ($n > 350$) was ever observed to produce an all male brood (male eggs are unfertilized), and all

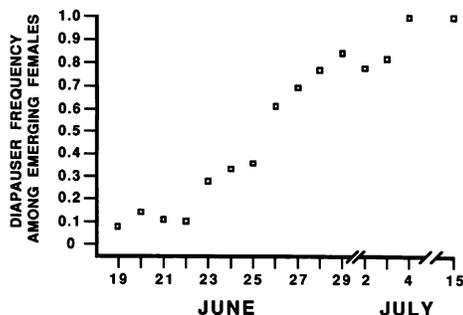


FIG. 1. Frequencies of presumed diapausing females (gynes; diapausers) emerging daily in the 1984 first brood. No emergence occurred on June 30 or July 1; all points are at 1.0 from July 4 through July 15.

foundresses dissected ($n > 85$) were inseminated. Thus, since males do not overwinter, foundresses must mate prior to diapause.

(iv) All foundresses were essentially unworn when they returned in the spring (no relation of wear and age). Thus, vanished first-brood females are inactive, presumably in diapause, from midsummer to the following April.

(v) Returning first-brood foundresses included females from throughout the previous first-brood emergence period (typically mid-June to mid-July), indicating an essentially complete overlap of the production schedules for diapausing and nondiapausing first-brood females (as in Fig. 1).

(vi) First-brood foundresses originated not only in nests containing eusocial or parasocial colonies but often in non-social (abandoned by emerging bees) nests, both with and without foundresses, which in a 1-year study would have appeared to be failures. In fact, these “failures” may often produce more gynes than some eusocial colonies.

(vii) The size distributions for all foundresses were not bimodal but often approximated normality (Fig. 2). Despite the overlap in their size distributions, second-brood foundresses were significantly larger than first-brood foundresses in all years ($P < 0.001$, t-test; see Table 1).

(viii) First-brood females typically accounted for some 50% of the returning foundresses (Table 1); the upper estimates given are probably closer to the actual figures.

(ix) An outbreak of pathogens (largely fungal) in midsummer of 1985 disproportionately affected the production of the second brood (100% failure in some nests), strongly favoring those foundresses who had *not* retained their daughters as workers. The outbreak persisted through 1986, resulting in an almost complete loss of the second brood of that year. In both years, first-brood diapausing bees acting solitarily avoided catastrophic midseason mortality.

DISCUSSION

Production of Reproductives. Theories regarding the timing of production of reproductives in social bees and wasps have long been based on the assumption of a rapid switch from worker-only to gyne and male production late in the colony cycle (“bang-bang control”; refs. 13 and 14). However, for wasps there is increasing empirical evidence that worker and reproductive production are often not temporally discrete (“graded control”; refs. 15–17). To date, social halictids have been viewed as “bang-bang” strategists, but the present study suggests this assumption has persisted largely because of the absence of detailed long-term observations.

Early production of diapausing females (especially if they overwinter away from the nesting site) could offer a signifi-

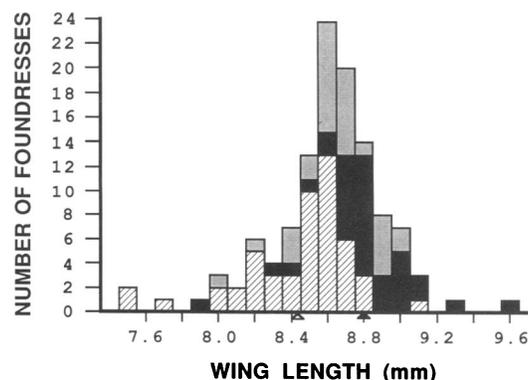


FIG. 2. Size distribution of 1985 spring foundresses. □, Foundresses from 1984 first brood ($n = 51$); ■, foundresses from 1984 second brood ($n = 35$); ▨, unmarked foundresses ($n = 31$); Δ and ▲, means for first and second brood females, respectively.

Table 1. Compositions of spring foundress pools for 1983–1986, including size ranges (wing length) and the estimated percentages of first-brood foundresses

| Foundresses | 1983 | 1984 | 1985 | 1986 |
|----------------------------|------------------------------|------------------------------|-------------------------------|------------------------------|
| Marked first-brood | | | | |
| Size, mm | | | | |
| Mean \pm SEM | ? | 8.19 \pm 0.07 ($n = 30$) | 8.43 \pm 0.05 ($n = 51$) | 8.38 \pm 0.05 ($n = 30$) |
| Range | ? | 7.4–8.9 | 7.5–9.1 | 7.8–8.7 |
| Marked second-brood | | | | |
| Size, mm | | | | |
| Mean \pm SEM | ? | 8.49 \pm 0.08 ($n = 9$) | 8.79 \pm 0.05 ($n = 35$) | 8.71 \pm 0.06 ($n = 12$) |
| Range | ? | 8.1–8.9 | 7.9–9.6 | 8.2–8.9 |
| Total | | | | |
| No. | 126 | 93 | 122 | 46 |
| Size, mm | | | | |
| Mean \pm SEM | 8.36 \pm 0.04 ($n = 62$) | 8.36 \pm 0.04 ($n = 92$) | 8.60 \pm 0.03 ($n = 117$) | 8.46 \pm 0.04 ($n = 44$) |
| Range | 7.4–9.0 | 7.4–9.1 | 7.5–9.6 | 7.8–8.9 |
| % first-brood foundresses* | 20–58% | 40–63% | 43–59% | 70–72% |

*The lower percentage limits given are based on the number of females definitely classified as first-brood bees; the upper percentage limits include that fraction of the unmarked foundresses that was estimated to be from the first brood, based on the known size distributions of both broods.

cant margin of security for bees, such as *H. rubicundus*, which often nest in disturbed, unstable environments. The assumptions of the “bang-bang” optimality model for reproductive production (13, 14) are violated by such stochastic environmental factors. The almost simultaneous cessation of provisioning by workers in temperate halictid populations greatly reduces the effective value of late-emerging workers, and this would also select for an earlier “switch” to gyne production than otherwise predicted. Therefore, one might expect graded control (manifested as early gyne production) to be common in halictids, as in other social Hymenoptera (16, 17).

Social Plasticity. The variation in colony social structure in this population seems to be largely due to mortality and dispersal and appears stochastic in nature. Parasocial nests result from foundress death, and nonsocial nests simply appear to occur when, by chance, all female progeny in a nest leave to enter diapause. Such an event is most likely in nests with small broods; for example, 13 of 14 nonsocial nests in 1984 had less than the average number of females. Therefore, social plasticity appears to be more of a demographic artifact than controlled behavioral variation.

Castes and Diapause. Caste differentiation in *H. rubicundus* appears to be imaginal and behavioral (there is no evidence for predetermined morphological or physiological caste differences). The two classes of females, those with or without diapause behavior, demonstrate what might be termed “diapause polyethism,” defined as differential entry into diapause among equivalent adults of the same cohort. As shown elsewhere (unpublished data), it appears that mating within the first days of adult life is crucial for diapause initiation in *H. rubicundus*; females that do not mate promptly become workers or replacement queens and do not diapause, even if they mate later.

For species such as this in which diapause is optional and induced early in adult life, control of diapause represents the first crucial deterministic “switch” in caste determination, for the discrete alternative behaviors irreversibly limit subsequent behavioral options. The diapausing and nondiapausing behavioral classes can be considered castes, which (following Eickwort and Kukuk; ref. 18) can be termed “gynes” and “nongynes,” respectively. In fact, it appears that gynes are more distinct from nongynes than are the subclasses within nongynes (workers and replacement queens) from one another; the primary functions of gynes are dispersal, colony initiation, and reproduction (after mating and overwintering), while nongynes function in maintenance

of existing colonies, do not diapause, and do not necessarily mate (reproductive nongynes, if they occur, are quite different from reproductive gynes).

Reports suggestive of diapause polyethism can be found in some previous studies. First-brood females of *Lasioglossum (Evyllaes) duplex* in Japan were found in diapause along with year-old foundresses (19), but actual survival of such bees was not established. It was reported that 36% of the first brood of this species vanished unaccountably (2), a remarkable parallel to the present study. In the closely related *Lasioglossum (Evyllaes) calceatum*, overwintering of old foundresses and possible first-brood females was again documented (20), and it was suggested that such bees might found nests in spring. Bonelli (21) and Plateaux-Quénu (22), studying this species in Europe, came to similar but equivocal conclusions as to overwintering of inactive first-brood females (C. D. Michener, personal communication). In a laboratory study of *Lasioglossum (Evyllaes) nigripes* (23), the mating and subsequent diapause of a presumptive worker was documented, but this was regarded as anomalous behavior. Packer (24) recorded inactive first-brood females of *Halictus ligatus* apparently entering diapause at the end of the season in Ontario; such bees may become auxiliaries in spring foundress associations or found nests independently. In *Halictus scabiosae* there appears to be a similar class of females (25), and a gradual switch from worker to gyne production has been indicated in this species (26), as for *H. ligatus* (6).

Theoretical and Evolutionary Considerations. It is true, of course, that the few species that produce no males in their first brood probably do not exhibit diapause polyethism, but considering the findings above and the inappreciability of diapause polyethism to all but a lengthy mark-recapture program, we should reevaluate the assumption of nonoverlapping caste production and theories based upon it. Present models of sex ratio and social evolution, for example (8, 27, 28), make no provisions for the overwintering of mated first-brood females, a feature that would dramatically alter the dynamics and predictions of these models.

Early diapause should not be looked upon as an evolutionary novelty. The early departure and diapause of daughters is typical in solitary, univoltine bees and wasps, including halictids, and can be considered ancestral (29). Facultative elimination of diapause may be the central issue in the evolution of a worker caste, for solitary, univoltine species with long-lived foundresses that develop the capacity to retain a few nondiapausing daughters could become social

and partially bivoltine in one step. Conversely, under conditions where a worker brood is not desirable or feasible, social species could easily revert to solitary behavior (social atavism), suggested, for example, by *L. (E.) calceatum*, which is solitary and univoltine at high altitudes in Japan (19). Notably, *H. rubicundus* is a species that traversed the Bering land bridge into North America (7) and was presumably univoltine in such northern latitudes, resuming social behavior and partial bivoltinism as it spread southward.

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