

## **A Test of the Mating Limitation Hypothesis for Caste Determination in *Evylaeus albipes* (Hymenoptera: Halictidae), a Primitively Eusocial Halictine Bee**

Cecile Plateaux-Quénu<sup>1</sup> and Laurence Packer<sup>2,3</sup>

Accepted September 17, 1997; revised October 1, 1997

---

*Yanega's (1997) mating limitation hypothesis (MLH) states that "if a female mates promptly after emerging, she then becomes a member of the maximally reproductive behavioral caste" (i.e., in most cases an overwintering gyne). Females that do not mate early become workers. We tested the MLH in laboratory colonies of a eusocial population of *Evylaeus albipes*. Of 24 worker brood females (13 from queenright and 11 from orphaned nests), 13 mated on the first day of flight activity and all mated within the first 5 days; there were no significant differences between mating rates of females from the two colony types. All 24 commenced foraging as workers after an average of between 3 and 4 days postmating. We conclude that the MLH does not apply to this species despite the fact that the only known halictine for which this hypothesis has been experimentally tested is the fairly closely related *E. marginatus*.*

---

**KEY WORDS:** social evolution; caste determination; mating; halictine bee.

### **INTRODUCTION**

The problem of the evolution of eusociality in insects is intimately related to the question of caste determination. In many primitively eusocial insects, caste is determined behaviorally through physical domination of workers by queens (Breed et al., 1978; West-Eberhard, 1969; Wheeler, 1986; Seger, 1991). In

<sup>1</sup>Laboratoire de Biologie et Physiologie du Comportement, URA, CNRS 1293, Université de Nancy I, BP 239, 54506 Vandoeuvre-lès-Nancy, Cedex, France.

<sup>2</sup>Department of Biology and Faculty of Environmental Studies, York University, 4700 Keele Street, North York, Ontario M3J 1P3, Canada.

<sup>3</sup>To whom correspondence should be addressed. e-mail: bugsrus@yorku.ca.

contrast, many or most of the advanced eusocial species use more subtle pheromonal caste determination mechanisms (Wheeler, 1986; Hartfelder, 1990; Winston, 1987). However, to understand the origins of eusocial behavior, caste determination in primitively eusocial insects needs to be investigated. As has been pointed out repeatedly (e.g., Knerer, 1980; Michener, 1990; Sakagami, 1974), the halictine bees are particularly good candidates for such studies because of their apparently multiple repeated and perhaps recent switches between solitary and eusocial behavior (reviewed by Packer, 1997). Factors that have been suggested to explain caste differentiation in these bees include behavioral domination, nutritional effects, and mating (reviewed by Michener, 1990; see also Richards and Packer, 1994; Yanega, 1997).

A general hypothesis to explain caste differentiation in social halictine species has been put forward by Yanega (1997). His "mating limitation hypothesis" (henceforth MLH) states that, for a species with facultative caste determination, "If a female mates promptly after emerging, she then becomes a member of the maximally-reproductive behavioral caste." The "maximally reproductive caste" consists of diapausing gynes in temperate halictines.

The MLH was put forward as a result of observations made on a population of *Halictus rubicundus* in New York (Yanega, 1988, 1989, 1997). This population has a colony cycle similar in many ways to that of a typical primitively eusocial sweat bee: overwintered females initiate nests in spring and produce a "worker" brood, the workers of which, in summer, provision a second brood consisting of males and females which eclose in late summer and mate and the latter overwinter to start the cycle again the following year. However, as a result of unusually painstaking observations, Yanega (1988) showed that a varying proportion of "worker" brood females disappeared from the study site soon after emergence in midsummer only to return the following spring to behave as nest foundresses. This mixing of worker and reproductive females in the brood produced during the spring solitary nesting phase when only foundresses were active was an unexpected finding. Regarding the mechanism of caste determination, Yanega (1989) noted a correlation between the abundance of males on a given day and the proportion of worker brood females emerging that same day that entered diapause (e.g., those which disappeared from the study site soon after emergence but which reappeared as foundresses the following year). The MLH elevates the observed day-to-day correlation between male abundance and the proportion of worker brood females that enter early diapause as a causation: mating soon after emergence results in a totipotent female becoming a potential queen (overwintering gyne), whereas not mating in the first few days as a flying adult leads to a female becoming a worker. Although large numbers of mated workers have been observed in most eusocial halictines (reviewed by Michener, 1990), Yanega (1997) suggests that these result from mating at some

greater time after eclosion as adults, i.e., that there is a window of opportunity during which mating or not mating will influence a female's caste but that, after this time, her caste is fixed. For *Halictus rubicundus* in New York, 4 days was considered the approximate upper limit for an unmated female to become mated and thereby enter diapause rather than becoming a worker (Yanega, 1989), the majority of diapausing females mated in 1 or 2 days.

In this paper we test the mate limitation hypothesis in the primitively eusocial species *Evylaeus albipes* reared under laboratory conditions. This species, like *Halictus rubicundus* (Eickwort *et al.*, 1996), has populations which are either predominantly or only solitary and others which are largely or entirely primitively eusocial (von der Heide, 1992; Plateaux-Quénu, 1989, 1993; Plateaux-Quénu *et al.*, 1997). Additionally, *E. albipes* is quite closely related to *E. marginatus* (Packer, 1991, 1997), the only perennially eusocial halictine and the only species for which the influence of mating upon caste determination has been verified experimentally (Plateaux-Quénu, 1960). Hence *E. albipes* seems to be a particularly promising candidate species for the detection of the MLH in another species.

## METHODS

### General Background Information

*Evylaeus albipes* has been studied in the laboratory and in the field (summarized by Plateaux-Quénu *et al.*, 1997). Field observations have not been made of nest sites but collections of females at various times of year from flowers have permitted estimation of some sociobiologically relevant variables. In eastern France, *E. albipes* is solitary and this behavior is maintained when females are brought into the laboratory and reared under warmer, long summer conditions typical of eusocial populations in the Southwest of the country. In the Southwest, one worker brood is produced and its foragers averaged 5% smaller than the overwintered females of the maternal generation; 67% of them had mated but only 6% had developed ovaries (Plateaux-Quénu *et al.*, 1997). Dissections of laboratory-reared workers also suggest oviposition to be monopolized by queens in matrilineal societies (i.e., those with foundress mothers, the queen still alive). Eusociality was maintained when bees of the social population were placed under laboratory conditions that simulated the cold, short-summer conditions of the solitary population. Under laboratory conditions, large numbers of males are produced in the "worker" brood (Plateaux-Quénu, 1989), and as noted above, in the field large numbers of workers are found to have mated, suggesting that some females may mate soon enough after emergence for the MLH to apply.

### Rearing Methods

Details of the methods used in the laboratory have been given elsewhere (Plateaux-Quénu, 1992; Plateaux-Quénu *et al.*, 1997). Here we reiterate the main points of relevance to the matter at hand. Foundresses were obtained from Les Eyzies and taken to the laboratory in Paris. Under laboratory conditions, the temperature, light intensity, and day length are controlled to mimic natural conditions as closely as feasible. Day length was increased up until the end of June and decreased thereafter (see Table II of Plateaux-Quénu 1992 and temperatures at the soil surface and at the brood cell level were measured (Table 3, Plateaux-Quénu *et al.*, 1997).

Males spent their entire adult lives (of about 1 month or more) in their natal cages unless they were transferred to another cage. In the latter instance, experimentally orphaned colonies composed of pupae of future worker brood females are generally settled in individual cages into which males produced by foundresses from the same population were introduced before female eclosion. These males were either taken as adults from another cage soon after eclosion or introduced as pupae, thereby ensuring that they have not mated before. Approximately equal numbers of males were introduced from each of these two sources and the numbers added to each cage approximated the number of worker brood females therein.

### Observations

Because studies of *E. albipes* concerned large numbers of individuals and colonies over an 11-year period, relatively few emerging females were observed until they mated and then had their caste fate followed also. However, the MLH states that mating soon after emergence determines a female's caste as a gyne, and consequently, any female that mates within the first few days of flight is not expected to become a worker. We obtained data suitable to test the MLH on 13 worker brood females from 8 eusocial nests and 11 females from 10 experimentally orphaned nests.

Observations of mating behavior in the laboratory indicated that males were as active in their attempts at copulating with the young workers as they were with the future foundresses. Multiple copulations of females of both castes were frequently observed, as was the presence of two or three males all trying to mate with the same worker or gyne. In some instances, males had to be removed from cages after females had become workers so that foraging could occur without repeated interruption.

### RESULTS

Table I presents the date of first emergence from the nest, date of first copulation, and date of first foraging for 13 worker brood females from matri-

**Table I.** Date of Emergence, Number of Days Between Emergence and Copulation, And Number of Days Between Copulation and Foraging for 13 *Evyllaeus albipes* Females Which Became Workers in Queenright Nests

Nest of origin (year) foraging	Female No.	Date of first emergence	No. of days between	
			Emergence & copulation	Copulation & foraging
31 (1993)	1	May 27	3	5
64 (1989)	1	May 27	0	6
64 (1989)	2	May 30	3	0
64 (1989)	3	May 30	3	1
64 (1989)	4	June 2	0	11
35 (1988)	1	June 15	0	6
35 (1988)	2	June 24	0	1
51 (1992)	1	June 23	0	4
51 (1992)	2	June 24	0	3
03 (1988)	1	July 2	1	1
20 (1984)	1	July 5	0	1
23 (1984)	1	July 8	0	7
24 (1984)	1	July 16	0	3

filial colonies; the latter two dates are expressed as the number of days since first emergence. Table II presents the same data for experimentally orphaned societies.

Nine of the 13 (69%) females from matrifilial societies mated on the first day after leaving the nest, 1 mated on the next day, and 3 mated 3 days after their first flight, giving an average of 0.77 day between emergence from the nest and mating. One female began foraging on the same day that she mated, three began the day after, and the average number of days passing between mating and the initiation of foraging was 3.8, with a maximum of 11.

For the orphaned worker brood females, only one individual observed became reproductively dominant within a semisocial society; this bee mated the day after her first flight (data not shown in Table II). This individual is a replacement queen and not a gyne: future gynes in *E. albipes*, as in other halictines, are unable to lay eggs before overwintering. Of the 11 bees that became workers, 4 mated on their first day out of the nest and 2 did so the day after. On average, 1.6 days passed between emergence and mating in bees that became workers. Three of these 11 bees foraged on the same day that they mated, with an average of 3.4 days elapsing between mating and pollen collection, again with a maximum of 11. Two of the worker bees that started foraging were observed closely enough that times of both mating and first foraging were exactly documented. One began foraging 3 h after mating; the other waited only 15 min after mating before pollen collection commenced.

Mann-Whitney *U* tests of the difference in the rapidity of mating between

**Table II.** Date of Emergence, Number of Days Between Emergence and Copulation and Number of Days Between Copulation and Foraging for 11 *Evylaeus albipes* Females Which Became Workers in Orphaned Nests

Nest of origin (year) foraging	Female No.	Date of first emergence	No. of days between	
			Emergence & copulation	Copulation & foraging
39 (1988)	1	June 17th	0	8
42 (1994)	1	June 22nd	1	3
60 (1989)	1	June 25th	0	6
65 (1990)	1	June 28th	4	0
37 (1993)	1	July 1st	3	0
E2 (1992)	1	July 7th	1	4
E2 (1992)	2	July 8th	0	11
30 (1991)	1	July 13th	0	6
C1 (1994)	1	July 20th	2	0 <sup>a</sup>
A1 (1991)	1	August 3rd	5	0
DD1 (1994)	1	August 7th	2	0 <sup>b</sup>

<sup>a</sup>This is the bee that foraged 3 h after its first mating.

<sup>b</sup>This is the bee that foraged 15 min after its first mating.

matrifilial and orphaned nests are not significant ( $U = 90.5$ ,  $P > 0.05$ ). Similarly, the duration elapsing between mating and foraging is not significantly different between workers in the two types of nest ( $U = 82.5$ ,  $P > 0.1$ ).

## DISCUSSION

For a full understanding of the origins of social behavior in insects, it is essential that caste determining mechanisms be elucidated. Yanega's (1988, 1997) MLH ascribes a causation between mating and caste in temperate social halictine species; bees that mate soon after emergence become diapausing gynes, and those that mate later or not at all become workers.

Our results indicate that mating soon after emergence as an adult does not induce diapause in laboratory colonies of a primitively eusocial population of *E. albipes*. The average duration between first emergence from the nest and mating was less than 1 day for worker brood females in eusocial societies and less than 2 days in those from semisocial (orphaned) colonies. All 24 of these bees became workers beginning foraging an average of 3–4 days after mating. None foraged before mating.

Our conclusions are based upon the results of laboratory experimentation. Yanega (1997) explicitly states why such results are unlikely to provide adequate tests of the MLH as follows: (1) unnatural photoperiods and temperatures are

sometimes used, (2) the spatial structure of bees in laboratory conditions may profoundly affect male–female encounter dynamics, and (3) laboratory conditions do not permit females to enter midseason diapause away from the natal nest. We deal with each of these issues in turn.

(1) Experimental conditions were designed to reflect natural ones as much as possible. Although in the absence of detailed studies at nest sites of this species in the field, it is not possible to state whether the laboratory temperature conditions were atypical, it is highly unlikely that they fall outside the range experienced by this species in the unpredictable climate of Southwest France. Furthermore, bees from social populations remain social under abiotic conditions typical of a solitary population and bees from the solitary population remain solitary under conditions typical of the social population (Plateaux-Quénu *et al.*, 1997). This suggests that the behavioral patterns of disparate populations of this species are somewhat buffered against quite different environmental conditions.

(2) The “interaction dynamics” between male and female halictids cannot be documented precisely under field conditions; they will vary day by day based upon phenology and weather and between sites based upon local topography, interaction site choice (of both males and females), and nest density (which will change markedly over time even within an aggregation). In the field only two-thirds of a sample of *E. albipes* workers had mated (Plateaux-Quénu *et al.*, 1997). However, as these were collected in early July, it is possible that a later collection would have yielded a greater proportion of mated workers. In comparison, all of the subsample of 40 workers that have been dissected in our laboratory studies had mated. Further, as males were present in the rearing cages throughout the period of worker activity, workers may have had a greater opportunity to mate soon after emergence in the laboratory than in the field. Under these conditions it should be impossible to produce workers if the MLH were operating, as males are active in rearing cages at the time the first brood females first leave their natal nests. According to Yanega’s arguments, these conditions should result in the species having as solitary individuals as long as condition 3 is met. Note, further, that it would seem that the only way to test the MLH experimentally in the field would be to alter the interaction dynamics (for example, by rearing some males in the laboratory and releasing them at the field site earlier than they would emerge under natural conditions). The requirement that male–female interaction dynamics be uninfluenced by the investigator precludes experimental test of the MLH under both field and laboratory conditions.

(3) That laboratory conditions should permit worker brood females to overwinter away from the nest site presupposes that, under natural conditions, they do indeed overwinter away from the natal nest. Although this is true of *Halictus rubicundus* in New York and some other halictines (Packer, 1993), it is certainly not the case for many species which overwinter beneath the natal nest (e.g., Packer and Knerer, 1985, 1986). Our experiments indicate that females of

*E. albipes* that are attempting to overwinter readily enter diapause in the soil beneath their natal nest in laboratory cages (Plateaux-Quénu *et al.*, 1997), as do some other species of the subgenus under natural conditions (Packer and Knerer, 1985). Furthermore, we have successfully raised brood from 16 overwintered females which were themselves reared in the laboratory, excavated hibernacula beneath their natal nest, and overwintered in a refrigerator (Plateaux-Quénu *et al.*, 1997). Consequently, if early-diapausing females had been produced in our cages, they would have had the opportunity to enter diapause under conditions sufficiently natural to be suitable for their later emerging conspecifics to overwinter successfully. Additionally, we have described behavioral differences between newly emerged workers and diapausing females (Plateaux-Quénu *et al.*, 1997) that enable us to recognize the bees to caste whether they are attempting to overwinter or not: worker females are much more lively than gynes from the first day of activity. This has been noted in laboratory studies of other eusocial species including *E. calceatus* (Plateaux-Quénu, 1978, 1985) and *E. nigripes* (Plateaux-Quénu, unpublished observation), both of which are in the same species group as *E. albipes*. In the latter species, under the rearing conditions described by Plateaux-Quénu (1965), one worker was observed to mate on the first day of emergence from the nest; it then immediately began collecting pollen.

The finding that newly emerged gynes have larger fat bodies than those of newly emerged workers (e.g., Plateaux-Quénu *et al.*, 1985; Knerer, 1992; Richards and Packer, 1994) also suggests that the propensity to overwinter and thereby become a member of the “maximally reproductive caste” is not entirely determined by mating alone but is influenced by something before females leave their natal nest. It would be interesting to investigate the size of the fat body of newly emerged female *Halictus rubicundus* at various stages during the emergence of both broods to investigate whether there is an increase in fat concentration that mirrors the temporal pattern of females becoming overwintering gynes.

In summary, we would argue that our experiments have taken place under conditions that are not expected to be outside the range experienced by this species in the wild. Consequently, we conclude that the MLH does not apply to *E. albipes* and, consequently, is not of universal applicability to primitively eusocial halictines.

Nonetheless, the mating behavior of sweat bees is highly variable both within and between species (Barrows, 1975a, b) and its role in influencing caste remains poorly understood. But there is one species for which mating is known, through experimentation, to determine caste: *Evylaeus marginatus*. This species was studied in detail by Plateaux-Quénu (1959). This is the uniquely perennial halictine with colonies lasting for 5 or 6 years, with one worker brood per year which is active in spring. Males are found only in the autumn at a time when

females have never been observed in flight. Mating takes place within the natal cells of the females, and only colonies in their final year are open to permit the egress of males and, consequently, are open to permit males from other nests to enter and mate with the females within. By experimentally opening a 3-year-old nest, Plateaux-Quénu (1960) obtained females which were destined to become workers but which, instead, mated and initiated new nests as potential queens the following spring. This overwintering of newly produced workers is indicative of a physiological similarity between the castes in this species, which is completely different from the situation in halictine species with an annual colony cycle.

It is somewhat surprising to find that the MLH does not apply in a species as weakly eusocial as *E. albipes*, which has (i) a large proportion of males in the worker brood and (ii) a large proportion of mated worker brood females under field as well as laboratory conditions. Furthermore, this species is fairly closely related to *E. marginatus* (Packer, 1991), in which mating does influence caste. It would seem that experimental verification of the MLH would be worthwhile in the species for which it was originally suggested.

#### ACKNOWLEDGMENTS

L. Packer's contribution to this study was aided by an NSERC research grant and C. Plateaux-Quénu's research was funded by CNRS URA 1293. We thank Dough Yanega for a preprint of his 1997 article and for discussion.

#### REFERENCES

- Barrows, E. M. (1975a). Mating behavior in halictine bees (Hymenoptera: Halictidae): II. Microterritorial and patrolling behavior in males of *Lasioglossum rohweri*. *Z. Tierpsychol.* **40**: 379-389.
- Barrows, E. M. (1975b). Mating behavior in Halictine bees (Hymenoptera: Halictidae): III. Copulatory behavior and olfactory communication. *Insectes Soc.* **22**: 307-332.
- Breed, M. D., Silverman, J. M., and Bell, W. J. (1978). Agonistic behaviour, social interactions and behavioural specialization in a primitively eusocial bee. *Insectes Soc.* **25**: 351-364.
- Eickwort, G. C., Eickwort, J. M., Gordon, J., and Eickwort, M. K. (1996). Solitary behaviour in a high altitude population of the social sweat bee *Halictus rubicundus* (Hymenoptera: Halictidae). *Behav. Ecol. Sociobiol.* **38**: 227-233.
- Hartfelder, K. (1990). Regulatory steps in caste development of eusocial bees. In Engels, W. (ed.), *Social Insects: An Evolutionary Approach to Castes and Reproduction*, Springer-Verlag, Berlin, pp. 245-264.
- Knerer, G. (1980). Biologie und Sozialverhalten von Bienenarten der Gattung *Halictus* Latreille (Hymenoptera, Halictidae). *Zool. Jb., Syst.* **107**: 511-536.
- Knerer, G. (1992). The biology and social behaviour of *Evylaeus malachurus* (K.) (Hymenoptera: Halictidae) in different climatic regions in Europe. *Zool. Jb., Syst.* **119**: 261-290.
- Michener, C. D. (1990). Reproduction and caste in social halictine bees. In Engels, W. (ed.), *Social Insects: An Evolutionary Approach to Castes and Reproduction*, Springer-Verlag, Berlin, pp. 77-122.
- Packer, L. (1991). The evolution of social behaviour and nest architecture in sweat bees of the

- subgenus *Evyllaes* (Hymenoptera: Halictidae): A phylogenetic approach. *Behav. Ecol. Sociobiol.* **27**: 339–344.
- Packer, L. (1993). Multiple foundress associations in sweat bees. In Keller, L. (ed.), *Queen Number and Sociality in Insects*, Oxford Scientific, Oxford. pp. 215–233.
- Packer, L. (1997). The relevance of phylogenetic systematics to biology: Examples from medicine and behavioural ecology. *Memoirs Mus. nat. Hist. Paris* **173**: 11–29.
- Packer, L., and Knerer, G. (1985). Social evolution and its correlates in bees of the subgenus *Evyllaes* (Hymenoptera: Halictidae). *Behav. Ecol. Sociobiol.* **17**: 143–149.
- Packer, L., and Knerer, G. (1986). An analysis of variation in the nest architecture of *Halictus ligatus* in Ontario. *Insectes Soc.* **33**: 190–205.
- Plateaux-Quénu, C. (1959). Un nouveau type de societe d'insectes: *Halictus marginatus* Brullé. *Ann. Biol.* **35**: 235–444.
- Plateaux-Quénu, C. (1960). Nouvelle preuve d'un déterminisme imaginal des castes chez *Halictus marginatus* Brullé. *C.R. Acad. Sci.* **250**: 4465–4466.
- Plateaux-Quénu, C. (1965). Sur le cycle biologique de *Halictus nigripes* Lep. *C.R. Acad. Sci. Paris* **260**: 2331–2333.
- Plateaux-Quénu, C. (1978). Les sexes de remplacement chez *Halictus calceatus* (Scop.) (Hym., Halictinae). *Insectes Soc.* **25**: 227–236.
- Plateaux-Quénu, C. (1985). Seconde couvée d'*Evyllaes calceatus* (Scop.) (Hym., Halictinae). les fondatrices sont-elles seules capables d'engendrer des fondatrices? *Ann. Sci. Nat. Zool.* **7**: 13–21.
- Plateaux-Quénu, C. (1989). Premières observations sur le caractère social d'*Evyllaes albipes* (F.) (Hymenoptera, Halictinae). *Actes Coll. Insectes Soc.* **5**: 335–344.
- Plateaux-Quénu, C. (1992). Comparative biological data in two closely related species: *Evyllaes calceatus* (Scop.) and *E. albipes* (F.) (Hym. Halictinae). *Insectes Soc.* **39**: 351–364.
- Plateaux-Quénu, C. (1993). Flexibilité social chez *Evyllaes albipes* (F.) (Hymenoptera, Halictinae). *Actes Coll. Insectes Soc.* **8**: 127–134.
- Plateaux-Quénu, C., Plateaux, L., and Packer, L. (1997). Differentiation between solitary and eusocial populations of *Evyllaes albipes* (F.) (Hymenoptera: Halictidae). I. Behaviour under experimentally reversed conditions (submitted for publication).
- Richards, M. H., and Packer, L. (1994). Trophic aspects of caste determination in *Halictus ligatus*, a primitively eusocial bee. *Behav. Ecol. Sociobiol.* **34**: 385–391.
- Sakagami, S. F. (1974). Sozialstruktur und Polymorphismus bei Furchen- und Schmalbienen (Halictidae). In Schmidt (ed.), *Sozialpolymorphismus bei Insekten*, Wissenschaft Verlagsgesell, Stuttgart, pp. 257–293.
- Seger, J. (1991). Cooperation and conflict in social insects. In Krebs, J. R., and Davies, N. B. (eds.), *Behavioural Ecology*, 3rd ed., Blackwell Scientific, Oxford, pp. 338–373.
- von der Heide, A. (1992). Zur bionomie von *Lasioglossum (Evyllaes) fratellum* (Perez) einer Furchenbiene mit ungewöhnlich langlebigen Weibchen (Hymenoptera, Halictinae). *Drosera* **1992**: 171–188.
- West-Eberhard, M. J. (1969). The social biology of polistine wasps. *Misc. Publ. Mus. Zool. Univ. Mich.* **140**: 1–100.
- Wheeler, D. E. (1986). Developmental and physiological determinants of caste in social Hymenoptera: Evolutionary implications. *Am. Nat.* **128**: 13–34.
- Winston, M. L. (1987). *The Biology of the Honeybee*, Belknap Press, Cambridge, MA.
- Yanega, D. (1988). Social plasticity and early-diapausing females in a primitively social bee. *Proc. Natl. Acad. Sci. USA* **85**: 4374–4377.
- 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. (1997). Demography and sociality in halictine bees (Hymenoptera: Halictidae). In Crespi, B. J., and Choe, J. (eds.), *The Evolution of Social Behavior in Insects and Arachnids*. Cambridge University Press, Cambridge (in press).