# Nesting Biology and Socially Polymorphic Behavior of the Sweat Bee *Halictus rubicundus* (Hymenoptera: Halictidae)

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**ABSTRACT**   *Halictus rubicundus* Christ is a facultatively social bee demonstrating solitary behavior in regions of cool climate, social behavior in areas of warmer climate, and a mixture of social and solitary behavior in marginal environments. In this article I compare original data to those from previously published studies of *H. rubicundus* in a variety of environments. I describe nest structure, nest density, bee size, reproductive output, sex ratio, and incidence of predators and parasites. From the patterns that emerge, I conclude that nest-site philopatry is important in structuring populations so that social behavior is favored over bivoltinism in warm climates. The sex ratio of populations is correlated with photoperiod but the relationship is not absolute; therefore, I propose that some other causal factor or a combination of factors, such as temperature or resource availability, is involved. The same mechanism may be responsible for changes in female size during the season. Differences in social behavior do not appear to provide a barrier to reproduction, and the presence of different forms does not imply incipient speciation.

**KEY WORDS**   *Halictus rubicundus,* social behavior, phenotypic plasticity, sex ratio, nest density, nesting biology

THE SWEAT BEE *Halictus rubicundus* Christ is widely distributed throughout the holarctic region. It is a fossorial bee, nesting primarily in sandy-loam soil with a south-facing aspect (Eickwort et al. 1996, Potts and Willmer 1997). Nests of this species are haplometrotic (founded by single females) (Yanega 1990) and often form dense aggregations (Eickwort et al. 1996, Hogendoorn and Leys 1997, Potts and Willmer 1998, Yanega 1990).

*Halictus rubicundus* demonstrates both social and solitary nesting behavior in different parts of its range, and in some cases in different nests of the same population. Social populations are typically found in areas of warm climate such as Kansas (Yanega 1993), southern Ontario (Knerer 1980), interior regions of The Netherlands (Hogendoorn and Leys 1997), and coastal British Columbia (Packer and Owen 1989). Solitary populations are typical of cooler climates such as Scotland (Potts and Willmer 1997), Alaska (Armbruster and Guinn 1989), and the mountains of Italy (Bonelli 1967) and Colorado (Eickwort et al. 1996).

To standardize terminology, I apply the following definitions to the specified terms (based on Eickwort and Kukuk 1986, Yanega 1989):

*Gyne.* Any potential nest foundress. A gyne must have the potential to undergo diapause. After she survives diapause, she may become a foundress, and if she produces workers she will become a queen.

*Foundress.* A *gyne* who initiates or attempts to initiate a nest after diapause. A foundress who becomes a dominant reproductive becomes a *foundress queen.*

*Nongyne.* A female that remains in an established colony and may or may not become reproductive. A nongyne does not have the potential to undergo diapause. This category includes workers and replacement queens.

*Worker.* A nongyne who remains in her natal nest to perform nest maintenance duties including foraging and guarding. A worker retains the ability to mate and in some cases lays eggs. I characterize a worker as one who collects a sufficient amount of pollen to provision at least one brood cell.

*Replacement Queen.* A nongyne who takes over as dominant egg layer upon the death or disappearance of the colony queen. The replacement queen is almost always mated and so is able to lay both fertilized and unfertilized eggs. A replacement queen may assume this role immediately upon emergence if there is no queen present, or she may first act as a worker and take over reproductive dominance upon the death of the queen.

**Life Cycle of *H. rubicundus*.** Nests of *H. rubicundus,* be they social or solitary, are often found in hard-packed bare sandy-loam soil. Nest entrances are typically associated with stones or tufts of vegetation on the ground surface, perhaps because of the heating

capacity of such objects (Potts and Willmer 1998). Females typically nest in dense aggregations, with upwards of 100 nests per square meter. Aggregations are believed to be made up of the nests of close relatives because nesting females demonstrate philopatric behavior (Yanega 1990, Potts and Willmer 1997).

Social populations of *H. rubicundus* have a life cycle typical of many halictid species (Michener 1990). Mated females emerge from hibernation in early spring and begin to excavate nests in bare soil. Gynes forage for pollen and nectar from a wide variety of plant species, especially those in the families Asteraceae and Rosaceae, to provision brood cells. A single egg is laid on each pollen ball, and a brood cell is sealed before construction begins for the next cell (Batra 1968). After 3–5 wk of provisioning the brood, a gyne will cease foraging. A 1- to 2-wk period of inactivity ensues at a nesting aggregation before the emergence of the first brood. The sex ratio of the first brood is female-biased containing 75–100% females (Yanega 1993). Upon emergence, most adult females from the first brood remain associated with their natal nest as foraging workers. There is no evidence for worker division of labor generating subcastes such as foragers or guards (Batra 1968). The nest foundress resumes laying eggs, now on pollen collected by her daughters. A queen also acts as principal guard in her nest, and she actively prevents workers from interfering with pollen loaf construction and brood-cell maintenance. The second brood is slightly male-biased (≈60%) and these males and females act as reproductives. Mating occurs on the ground surface in and around the nest aggregation. Males patrol in the vicinity of their natal nest and pounce upon females entering or leaving any nest in the area (Barrows 1976). Upon mating, females enter hibernation at some unknown location away from the nesting site (Sakagami and Michener 1962), and the foundresses, workers and males die at the end of the season.

For solitary populations, nesting begins in late May to mid-June. A gyne provisions a single brood made up of males and females (also ≈60% male). The timing of emergence of this brood roughly corresponds to that of the last brood in social populations. As in social populations, mated females enter hibernation away from nesting sites and males and nest foundresses die at the end of the season. The lack of a female worker brood defines this nesting habit as solitary.

In marginal environments, a mixture of social and solitary nests may be found in a single population. Observing the same population of *H. rubicundus* in New York over the course of 6 yr, Yanega (1993) determined that, on average, 35% of the gynes were effectively solitary in a given year (range, 24–56%), and that this was correlated with male production in the first brood. The mechanism he proposed to explain the social polyethism is as follows. Up to 25% of the first brood was composed of males, and these males had the opportunity to mate with first brood females. Furthermore, first-brood females who mated soon after emergence (i.e., <4 d) did not forage and instead entered diapause early only to return the following spring as nest foundresses. Unmated females remained in the natal nest as workers. Yanega (1992) termed this the mate-limitation hypothesis. Because some first-brood females became early-diapausing gynes, the worker force in this population was reduced, leaving some smaller nests without any workers (thus some nests were effectively solitary). He theorized that the propensity of a gyne to produce first-brood reproductives was not genetically controlled because foundresses who themselves were a member of the first brood were no more likely to have first-brood diapausing daughters than were foundresses from the second brood.

Social organization in *H. rubicundus*, therefore, can be viewed as a continuum, with the fraction of males in the first brood (and therefore the fraction of early-diapausing females) determining the degree of sociality in the population. Extending the theory further, Yanega (1993) proposed that the fraction of males in the first brood is dependent upon abiotic factors, primarily the photoperiod a gyne experiences at the time of egg-laying, with temperature playing a minor role. Yanega believes that higher temperatures are correlated with longer photoperiod but that photoperiod is the factor that serves as an environmental sex-ratio cue (Yanega 1993). He termed this the "environmental control hypothesis" (Yanega 1997). According to the environmental control hypothesis, reproductive females experiencing relatively short photoperiods, such as those in late March and April, lay mostly female eggs. As the daily photoperiod lengthens an egg-layer produces a greater number of male eggs. Therefore, foundresses in warm climates, who begin provisioning offspring in the spring near the equinox, first produce female-biased broods. With a few or no males in the first brood, most of the offspring necessarily function as workers, not because they physiologically differ from their mated sisters, but because the shortage of males leaves them unmated. As the season progresses toward the solstice, a gyne lays a greater proportion of male eggs. Thus, the second brood is likely to be male-biased, and all second-brood offspring will be reproductives. For populations in cooler climates, egg-laying commences in June when the days are long. Thus, the first (and only) brood is male-biased and all female offspring have the opportunity to mate and become gynes.

My goal is to characterize the nesting biology of social and solitary populations of *H. rubicundus* by summarizing previous work on this species and comparing it to my own investigations. In this article I describe various aspects of this species' life history and nesting biology, and I also address several theories put forth regarding the mechanisms underlying the facultative nature of its social biology. Finally, I discuss the implications of variations in nesting biology between social and solitary populations for the evolution of social behavior and the possibility of incipient speciation.

## Materials and Methods

I studied three solitary nesting aggregations (referred to as Kettle Pond, Beaver Pond, and Picnic Area) in the subalpine zone near Gothic, CO (altitude 2,850 m), on the western slope of the Rocky Mountains. I studied these populations from 5 June through 12 August 1998 and from 28 July through 11 August 1999. For contrasting social populations, I studied one nesting aggregation in Kaysville, UT (referred to as Kaysville Farm) and two in Logan, UT (referred to as Rock Garden and Green Canyon), from 3 May through 26 July 1999. These locations are in the northeastern section of Utah in the intermountain zone (altitude in Kaysville is 1,326 m and in Logan is 1,382 m).

In Colorado, the Kettle Pond aggregation covered an area ≈8 m long by 4 m wide, on a southwest-facing slope. The Beaver Pond aggregation was ≈9 m long by 5 m wide on a slope facing due south. The Picnic Area aggregation was ≈15 m long by 7 m wide on a contoured slope that faced from south to southwest. In Utah, the Kaysville Farm population was situated on level ground along a dirt road in a peach and apple orchard, and was ≈100 m long by 1.5 m wide. The Rock Garden population was located in a level rock garden ≈10 m long by 2 m wide in the southwest corner of a private corner lot in a suburban neighborhood. The Green Canyon aggregation was ≈4 m long by 3 m wide on a southwest-facing slope on public lands.

First, I calculated the density of nests in each population by throwing a 50 by 50 cm (in 1998) or 30 by 30 cm (in 1999) square quadrat a minimum of twelve times per nesting aggregation. I tossed the quadrat so that no part fell outside the aggregation, and so that multiple tosses did not cover the same patch of ground. I counted every nest entrance within the quadrat and converted all measurements to the number of nests per square meter (nests/m$^2$). For social populations I measured nest density in mid-May 1999 and again in early July 1999 and for solitary populations I measured nest density in late June 1998 and late July 1999.

As an indicator of bee size, I measured the headwidth (width of the head capsule plus the eyes) of recently killed bees (frozen or in ethanol) from each of the six populations using hand-held calipers. I measured a minimum of nine and a maximum of 32 individuals of a particular caste (gyne, nongyne) from a population within a 2-wk period. For social populations I measured the size of nesting gynes (foundresses; $N = 83$), first brood (B1) female offspring ($N = 56$), and second brood (B2) female offspring in 1999 ($N = 54$). For solitary populations I measured the size of foundresses ($N = 51$) and their female offspring ($N = 47$) in 1998.

To quantify reproductive output, parasite load, and sex ratio of a brood, I excavated a total of 142 nests from both social and solitary populations. At the social population at Kaysville Farm I excavated 31 nests during the first brood in late May 1999 and 21 nests during the second brood in late July 1999. In the area
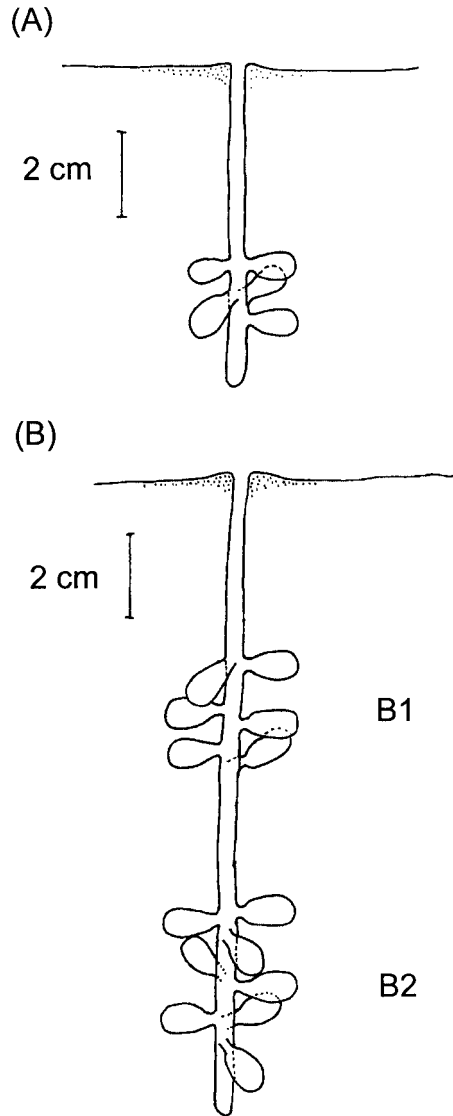


**Fig. 1.** Nest architecture of *Halictus rubicundus.* (A) A solitary nest. (B) A social nest. The two clusters of brood cells in the social nest correspond to the two broods (B1 and B2).

around Gothic I excavated a total of 48 nests (in the three focal populations plus several other locations) containing reproductive brood in late July 1998 and 42 nests containing reproductive brood in early August 1999.

To determine a social or solitary gyne's productivity during the reproductive brood, I counted the number of cells containing healthy, developing brood during July or August. To determine productivity during B1 in the social population I counted the number of cells containing healthy, developing brood during May 1999.

I measured parasite load and other sources of brood death by counting the number of cells containing

**Table 1. Nest density for three populations at each of two locations**

| Social structure | Year | Population | Nest-founding phase (N) | B2 Provisioning phase (N) |
|---|---|---|---|---|
| Social | 1999 | Kaysville Farm | 113.8 ± 7.12 (25)[a] | 89.3 ± 4.37 (27) |
|  |  | Rock Garden | 134.7 ± 9.19 (24) | 105.1 ± 6.71 (26) |
|  |  | Green Canyon | 93.5 ± 6.64 (17) | 72.2 ± 6.09 (16) |
| Solitary | 1998 | Picnic area | 27.6 ± 2.44 (20) | NA |
|  |  | Beaver Pond | 41.9 ± 2.20 (17) | NA |
|  |  | Kettle Pond | 24.8 ± 1.92 (15) | NA |
| Solitary | 1999 | Picnic area | 24.1 ± 3.27 (12) | NA |
|  |  | Beaver Pond | 38.1 ± 4.99 (14) | NA |
|  |  | Kettle Pond | 25.4 ± 3.72 (14) | NA |

NA, Not applicable.

[a] Densities are reported as nests/m$^2$ (mean ± SE).

natural enemies (mold, ants, fly larvae) and by counting the number of aborted cells and cells containing dead brood. It was unclear whether the natural enemies were the cause of brood death, or they were scavengers on brood that had died from other causes.

To calculate the sex ratio of the brood, I determined the sex of each developing offspring by visual inspection of pupae (males have more antennal segments and more dorsally visible abdominal segments than females). If developing brood were still in the larval stage, I reared them in the laboratory by placing them in depressions in wax-filled petri dishes until pupation.

## Results

**Nest Description.** Nesting aggregations of both social and solitary populations of *H. rubicundus* are typically constructed on south-facing slopes of sandy loam and some gravel. For solitary populations, a nest comprises a vertical burrow ≈7–12 cm deep with a series of cells attached perpendicularly to it (Fig. 1A). Cells are connected to the burrow by short (2–10 mm) lateral tunnels. For social populations, cells of the first brood are typically clustered together within a 10-cm section of soil and separated from the second brood by another tunnel extending ≈5–10 cm deeper into the substrate (Fig. 1B).

**Nest Density.** Nest density in the three social populations was highest during the nest-founding phase, and declined during the B2 provisioning phase. The density in the nest-founding phase was significantly higher than the B2 provisioning phase for all three populations (Table 1; *t*-test: Kaysville Farm *t* = 2.939, df = 48, *P* = 0.005; Rock Garden *t* = 2.636, df = 48, *P* = 0.011, Green Canyon *t* = 2.357, df = 31, *P* = 0.025). Density probably declined because some nests failed before any workers were produced, and no new nests were initiated after the end of the founding phase. Nest densities in all three of the solitary populations in both years were lower than the nest densities in any of social populations in either the founding or worker phases (Table 1).

The population of social and solitary nests studied by Yanega (1990) had a nest density of 34.10 nest/m$^2$ averaged across all years of the study. Potts and Willmer (1998), who studied 10 different solitary populations of *H. rubicundus* in Scotland, found aggrega-

tions to have nest densities ranging from 1 to 37 nests/m$^2$. Nest densities in very small areas (<10 cm$^2$) may be quite high in any given aggregation, however. The social Rock Garden population of this study had up to 333 nests/m$^2$, when measured with a 50 by 50 cm quadrat.

**Bee Size.** Foundresses collected from the three social populations had an average head-width of 3.10 ± 0.12 mm, which significantly exceeded that of first brood females from those populations (2.80 ± 0.12 mm; *t*-test: *t* = 14.48, df = 137, *P* < 0.001) but not that of the second brood (3.08 ± 0.14 mm; *t*-test: *t* = 0.86, df = 128, not significant). The size of foundresses from the three solitary populations (average headwidth = 2.58 ± 0.24 mm) was not significantly different from their daughters (2.57 ± 0.23 mm; *t*-test: *t* = 0.10, df = 93, not significant). Solitary females were smaller than any group from the social populations (Fig. 2).

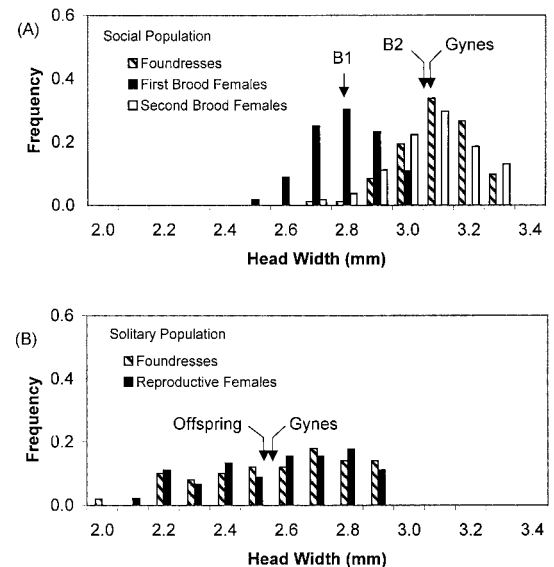**Reproductive Output.** There was an average of 6.06 ± 2.10 (range, 2–11) total brood cells per nest



**Fig. 2.** Histogram of headwidths for foundresses and offspring in populations of *H. rubicundus*. (A) Social populations. (B) Solitary populations. Arrows indicate means for each category.

**Table 2.  Reproductive output for nests in solitary populations across 3 yr**

| Population[a] | Type of nest (N) | Total cells[b] (Range) | Viable brood | Proportion of viable brood |
|---|---|---|---|---|
| Gothic, CO 1988 | With foundress (17) | 9.8 ± 0.81 (6–18) | 7.9 ± 0.85 | 0.95 |
| (Eickwort et al. 1996) | Without foundress (11) | 6.4 ± 1.28 (1–13) | 4.3 ± 1.13 | 0.56 |
| | Total (28) | 8.5 ± 0.76 (1–18) | 6.5 ± 0.75 | 0.84 |
| Gothic, CO 1998 | With foundress (28) | 4.3 ± 0.51 (3–9) | 3.2 ± 0.42 | 0.90 |
| | Without foundress (20) | 3.3 ± 0.39 (1–7) | 2.3 ± 0.40 | 0.66 |
| | Total (48) | 3.9 ± 0.31 (1–9) | 2.8 ± 0.30 | 0.72 |
| Gothic, CO 1999 | With foundress (25) | 6.3 ± 0.39 (3–10) | 5.2 ± 0.32 | 0.91 |
| | Without foundress (17) | 5.0 ± 0.32 (3–8) | 3.4 ± 0.28 | 0.64 |
| | Total (42) | 5.8 ± 0.28 (3–10) | 4.5 ± 0.26 | 0.77 |

[a] All nesting aggregations studied in 1998 and 1999 are the same, and are within 3 km of the population studied in 1988.
[b] Data are reported as mean ± SE.

during B1 of the social population at Kaysville Farm. The average number of brood cells per nest constructed during B2 was 11.67 ± 6.44 (range, 2–33) (this value does not include those cells that clearly were constructed during B1, usually separated from B2 cells by a 5–10 cm length of tunnel). At the time of excavation, there was an average of 4.39 ± 2.23 (range, 0–11) developing offspring in B1 for the social population at Kaysville Farm and an average of 10.52 ± 7.01 (0–33) in B2 of that population.

In the solitary populations the average number of total brood cells per nest in 1998 was 3.92 ± 2.13 (range, 1–9), which was significantly lower than that in the same populations in 1999 (5.79 ± 1.83, range 3–10; *t*-test: $t = 4.48$, df = 87, $P < 0.001$). The average number of developing, viable offspring in the only brood of the solitary populations was 2.81 ± 2.07 in 1998 and 4.48 ± 1.70 in 1999 (*t*-test: $t = 4.20$, df = 87, $P < 0.001$).

The reproductive output of solitary females at Gothic in 1998 and 1999 was less than that observed by Eickwort et al. (1996) in 1988 at the same location (Table 2). Despite the significant year-to-year variation in nest productivity at Gothic, some generalizations can be made. For instance, across all years, nests that retained their foundress until the emergence of the brood had much higher productivity than those that lost their foundress (Table 2). Two factors contribute to this advantage: there were fewer total cells per nest if a gyne died before the end of the provisioning phase, and a greater fraction of the total cells were viable if a gyne survived (gynes may have been able to prevent brood loss by defending or cleaning the nest).

In the social population at Kaysville in 1999, the first broods were as large as the single brood in Gothic, and had similar proportions of viable offspring (Table 3). However, the proportion of viable reproductive offspring (B2) across all nests in the social population is higher than the average across all solitary nests in 1998 or 1999.

A population of *H. rubicundus* in a marginal environment (New York) in 1984 had ≈6.7 B1 offspring per nest (range, 1–11), and 5.7 B2 offspring (Yanega 1989).

**Sex ratio.** In the social population at Kaysville Farm, there was an average of 3.94 ± 2.38 females and 0.45 ± 0.72 males per nest in B1 ($N = 31$), and 3.38 ± 2.44 females and 5.48 ± 6.22 males in B2 ($N = 21$). The overall population sex ratio during B1 was 0.11 male:female and for B2 it was 1.62 male:female.

For the solitary populations at Gothic there was an average of 1.08 ± 1.09 females and 1.58 ± 1.41 males per nest ($N = 48$) in 1998, resulting in a population sex ratio of 1.46 male:female. In 1999, there was an average of 1.62 ± 0.88 females and 2.62 ± 1.38 males per nest ($N = 42$) for a population sex ratio of 1.62 male: female.

Across populations, male:female sex ratio of progeny increases as days lengthen, just as predicted by Yanega's environmental control hypothesis (Yanega 1997). The sex ratio of B1 in the social Kaysville Farm population, in which eggs are laid from early April until early May, is clearly female biased, with only 10.3% of the population male. The B1 population in Queens, NY (egg production from early to late May 1984) was ≈25% male (Yanega 1989), and several populations that had egg production in mid-June to early July, whether they be the only brood in a solitary population or the second brood in a social population, had sex ratios that were ≈60% male (B2 Kaysville Farm [this study] = 62%, B2 Queens, NY [Yanega 1989], = 60%, 1988 Gothic, CO [Eickwort et al. 1996],

**Table 3.  Reproductive output for nests in representative social (Kaysville) and solitary (Gothic) populations in 1998 and 1999**

| Population | N | Total cells[a] (Range) | Viable brood (Range) | Proportion of viable brood |
|---|---|---|---|---|
| Gothic, CO 1998 | 48 | 3.9 ± 0.31 (1–9) | 2.8 ± 0.30 (0–9) | 0.72 |
| Gothic, CO 1999 | 42 | 5.8 ± 0.28 (3–10) | 4.5 ± 0.26 (1–10) | 0.77 |
| Kaysville, UT 1999 Brood 1 | 31 | 6.1 ± 0.38 (2–11) | 4.4 ± 0.40 (0–11) | 0.72 |
| Kaysville, UT 1999 Brood 2 | 21 | 11.7 ± 1.40 (2–33) | 10.5 ± 1.53 (0–33) | 0.90 |

[a] Data are reported as mean ± SE.

= 63%, 1998 Gothic, CO [this study], = 59%, 1999 Gothic, CO [this study] = 62%).

**Parasites and Predators.** At Kaysville Farm, 45.2% of the nests lost at least one brood cell to predators and parasites during B1, resulting in 27.7% of the brood being destroyed. In B2, 33.3% of the nests were affected, resulting in 9.8% of brood cells being destroyed. Mold was the most common type of natural enemy during B1 at Kaysville Farm, affecting 60.0% of dead brood, whereas flies and ants were the most common natural enemies during B2 (87.5% of brood death).

In 1998 at Gothic, 52.1% of all nests fell victim to some form of predation or parasitism, resulting in 28.2% of the population's brood being destroyed. In 1999 at this location, 69.0% of the nests were affected, resulting in a loss of 22.6% of the brood. In 1998, mold affected 68.2% of all brood, whereas in 1999 it affected 87.8% of the brood.

## Discussion

**Nest Density.** The density of nests in a given area appears to be site-specific, and not related to sociality. Caution should be used when drawing generalizations on nest density in relation to sociality because the sample sizes are small, sampling techniques are not uniform across studies, soil quality (and heterogeneity) may not be comparable across sites, and there may be biases in identifying aggregations if the densest ones are most likely to be discovered.

Potts and Willmer (1997) determined that small-scale differences in nest site quality, such as soil hardness and insolation, play a major role in nest density. These authors, along with Yanega (1990) emphasized the role that nest site philopatry plays in reinforcing nest founding in high quality habitat, in both social and solitary populations. High-quality nesting sites will generate more reproductives, and, assuming philopatric behavior, more females will return to that area the following spring. Philopatry occurs despite the fact that gynes of *H. rubicundus* overwinter away from the nesting aggregation (Sakagami and Michener 1962, Yanega 1990). For example, in a solitary population in Invergowrie, Scotland, Potts and Willmer (1997) reported a median foundress dispersal distance of 1.37 m from the natal nest, and in a social population in New York, Yanega (1990) found that the majority of foundresses initiated nests within 0.5 m of their natal nest (median = 0.27 m).

The fact that nest-site philopatry plays an important role in structuring bee populations may be significant for understanding why populations of *H. rubicundus* in warm climates are social and not bivoltine. Yanega (1990) noticed that not only is female dispersal limited, but male dispersal is also quite low. He observed males patrolling the immediate area around their natal nest in search of mating opportunities. Combined with the fact that foundresses who nest in close proximity are most likely sisters or cousins, it appears as though nesting aggregations may in fact represent very limited gene pools. With such low genetic diversity within

an aggregation and especially within a nest (future gynes may mate with their own brothers or cousins), relatedness asymmetry imposed by haplodiploidy approaches zero, and a B1 daughter will be highly related to all of her mother's offspring, including her own brothers. Therefore, the loss of inclusive fitness (Hamilton 1964) a B1 female experiences by rearing her mother's offspring rather than her own may be very slight, such that if there are limited mating opportunities (Yanega 1997) or maternal dominance due to size differences (S.L.S., unpublished data) or even the cost incurred by starting her own nest in mid-season, it may be to her advantage to remain in her natal nest as a worker. For a nest foundress, as long as she lives long enough to produce a second brood, it is to her advantage to retain daughters as workers because with their help she is able to produce more reproductives over the course of a season than she would alone (see below). The significance of inbreeding on the evolution of altruistic behavior has been demonstrated both theoretically (Hamilton 1972, Michod 1979, Uyenoyama 1984, Wade and Breden 1981) and empirically (Wade 1980).

**Bee Size.** The patterns of variation in bee size in *H. rubicundus* can be explained, at least in part, by temperature differences within and among locations during brood development. Several authors have noted a relationship between temperature and bee size for other bee species. Richards and Packer (1996) found that cooler temperatures in a given year resulted in smaller bee sizes compared with warmer seasons at the same location for *H. ligatus* Say. Yanega (1989) also noted that larger females of *H. rubicundus* were produced as the season progressed and the temperature increased. However, Plateaux-Quénu (1993) found that, for another halictine bee (*Lasioglossum (Evylaeus) calceatum* Scopoli), temperature was inversely related to worker size in laboratory-reared colonies. Kamm (1974) found the same pattern in natural populations of *L. (Dialictus) zephyrum* Smith. The different results can be reconciled if one assumes that there is an optimum temperature that produces maximum size, with smaller sizes at both higher and lower temperatures, due to various stresses. So under certain conditions an increase in temperature will lead to an increase in offspring size and under different conditions it will lead to a decrease. Another possibility is that temperature may have indirect effects on flowering and hence on cell provisioning. Lower temperatures in natural populations, resulting in lower resource availability, may cause smaller than average offspring sizes.

Given that the offspring size in *H. rubicundus* is correlated with temperature, one would expect to see greater size differentiation between queens and their workers in areas where this species nests over a long season, with a substantial temperature gradient throughout that season. Furthermore, size difference within a pair of females appears to be important in defining the repertoire of behaviors used by individual bees in an encounter (S.L.S., unpublished data); this in turn would affect dominance relationships between
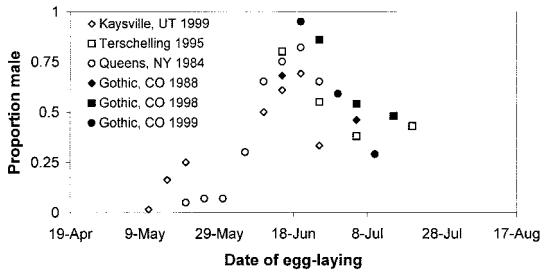
**Fig. 3.** Sex ratio of the brood on the approximate date that eggs were laid (Yanega 1993, Eickwort et al. 1996, Hogendoorn and Leys 1997).

gynes and their daughters. Indeed, this study and that of Yanega (1989) indicate that size difference and degree of sociality are greatest in areas with the longest growing season.

**Reproductive Output.** During the solitary phase of the social population in 1999, productivity and brood survival seems similar to that in solitary populations in all years. But, when one considers the reproductive broods, nests in social populations are more than twice as productive than nests in solitary populations, and they have greater survival probabilities for developing brood. These results suggest that a gyne who produces a worker brood and then a reproductive brood may produce more reproductive offspring (males and females) than a hypothetical gyne who produces two solitary broods in a single season. Data from multiple seasons in a social population are necessary to substantiate this point.

It appears that, in a marginal environment (Yanega 1989), despite a greater number of offspring in B1, a study population produced fewer B2 reproductives per first-brood offspring than did a social population in Utah. One must consider, however, that nearly half of all B1 females in the marginal environment are actually early-diapausing gynes (Yanega 1989), therefore the total number of reproductives must include offspring from both broods. Nevertheless, by reducing the worker force in favor of B1 reproductives, a nesting female lowers the number of potential reproductives throughout the season as a whole by sacrificing B2 productivity. This prompts the question: why would a gyne sacrifice higher reproductive output in the second brood in favor of fewer reproductives spread across two broods? Generating reproductives in the first brood may be a means of "bet hedging" (Seger and Brockmann 1987). Foundresses sacrifice workers who could help rear more offspring in B2, but in doing so they ensure the production of reproductive offspring in a marginal environment by laying both male and female eggs in the first brood.

**Sex Ratio.** Using information from previous studies of nest excavations that included the sex and developmental stages of brood in the nest at the time of excavation (Yanega 1993, Eickwort et al. 1996, Hogendoorn and Leys 1997), combined with the timing of development for *H. rubicundus* (Yanega 1993), I was able to infer the date that eggs were laid, and the

sex ratio of the brood at the time of egg-laying within approximately a 5-d time frame (Fig. 3). Indeed, as the environmental control hypothesis predicts, male production in all populations seems to peak at the solstice (given a margin of error for my estimation of the date that eggs were laid). Although male production may be tied to the relative length of the photoperiod, the relationship is not absolute. That is evidenced by the fact that Terschelling, Netherlands (Hogendoorn and Leys 1997) has longer days from 15 May through 30 July (15.5 h to 17 h.) than any of the other sites (14 to 15 h.), yet the fraction of male brood in that study population is not consistently higher than in any other population. Also, there may be significant year-to-year variation in the timing of male production that cannot be attributed to photoperiod alone (S.L.S., unpublished data).

The information gathered in this study, along with that of previous work on *H. rubicundus* and related species, can be used to draw some generalizations about the mechanisms underlying facultative sociality in this species, and the role of social variation in incipient speciation.

First, there is substantial evidence for environmental control of sex ratio in *H. rubicundus.* The fraction of males in a brood varies with the photoperiod at the time of egg-laying across many populations displaying a range of social behaviors. Because of this, a single mechanism can be invoked to explain variations in sex ratio, and perhaps sociality, across a range of climates. However, the relationship between photoperiod and sex ratio appears to be relative and not absolute. There is a female-biased sex ratio early in the season even at high latitudes such as in The Netherlands, despite daylengths that would provoke male production in lower-latitude locations across North America. Perhaps the response to photoperiod has diverged geographically; selection may adjust the response to photoperiod so that the phenology of the bees is appropriate for the local environment. However, year-to-year variations in the timing of male production indicate that photoperiod is not the only environmental cue involved (Yanega 1993). Manipulative experiments are critical for our understanding of this relationship.

The range of social behaviors exhibited by *H. rubicundus*, although perhaps driven by environmental factors, seems to be tailored so as to produce the maximum number of reproductives possible in each set of conditions. In the coldest climates, the growing season is not long enough for a gyne to produce sequential worker and reproductive broods, and a single reproductive brood may be her only opportunity to realize reproductive success (Sakagami and Packer 1994). In regions of marginal environments, with slightly longer growing seasons, the majority of gynes produce some workers (75% of nests) but many also produce some early diapausing gynes (Yanega 1989). In this way, foundresses can take advantage of workers to help them produce a larger reproductive brood than they could manage on their own, yet they still "hedge their bets" in the face of unfavorable conditions by

producing some early diapausing gynes. Finally, in very warm climates, gynes produce one (Yanega 1993) all-female worker brood, that helps to provision a reproductive brood. A gyne produces more reproductives with the help of workers than she would by provisioning two (or more) reproductive broods by herself.

In general, social flexibility in the face of various environmental conditions is well-documented within *H. rubicundus.* In all likelihood, facultative sociality has played a significant role in the persistence and dispersal of this species. If, as described above, populations of this species are able to adapt to local conditions by adjusting the timing of production of reproductive males and females, this species has the potential to colonize environments inaccessible to obligately social species, and to out-perform obligately solitary species in more favorable conditions. Indeed, the persistence of this species is evidenced by its ability to nest in disturbed areas such as gravel parking lots and footpaths, and in harsh mountain conditions near 3000 m. The flexible nature of its sociality has been implicated in its current holarctic distribution. Michener (1990) hypothesized that social populations in Asia were able to cross the Bering Land Bridge during the Pleistocene as solitary bees, before reverting to social behavior once more as they dispersed south in North America. The Rocky and Appalachian mountain ranges may represent trivial barriers to the dispersal of *H. rubicundus.*

Finally, there appears to be little distinction in the life history of social and solitary populations that would promote speciation of the two forms. Much evidence points to the flexible nature of sociality; variability is environmentally, and not genetically, determined. The timing of production of reproductives seems compatible for all populations of this species and should not pose a barrier to reproduction. However, one might look toward the role that limited dispersal plays in the isolation of populations, and eventual accumulation of reproductive isolating mechanisms.

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