VA@

College of William & Mary Interlibrary Loan



ILLiad TN: 232834

**Borrower:** VA@

**Lending String:** *VWM,VLW,VLR,VOD

**Patron:** McFrederick, Quinn

**Journal Title:** Behavioral ecology and sociobiology.

**Volume:** 38 **Issue:**
**Month/Year:** 1996 **Pages:** 227-233

**Article Author:**

**Article Title:** Eickwort, G. C., J. M. Eickwort, J. gordon,and M. A. Eickwort; Solitary behavior in a high altitude population of the social bee Halictus rubicubndus

**Imprint:** Berlin, New York, Springer-Verlag, 1976-

**ILL Number: 43890405**



**Call #:** QL750 .B533

**Location:** SWEM STACKS

**ARIEL**
**Charge**
**Maxcost:** $40IFM

**Shipping Address:**
VA@ - Alderman Library
Interlibrary Loans (VA@)
University of Virginia
160 N. McCormick Rd.
Charlottesville, VA 22904

**Fax:** 434-924-4337
**Ariel:** 128.143.166.41

SEND BY ODYSSEY

Behav Ecol Sociobiol (1996) 38 : 227–233

© Springer-Verlag 1996

George C. Eickwort · Jeffrey M. Eickwort
Jill Gordon · M. Alex Eickwort

# Solitary behavior in a high-altitude population of the social sweat bee *Halictus rubicundus* (Hymenoptera: Halictidae)

NOTICE: This Material
may be protected by copyright
law. (Title 17 US Code)

Received: 4 November 1994/Accepted after revision: 23 October 1995

**Abstract** In the subalpine region of the Rocky Mountains of Colorado, United States, *Halictus rubicundus* has a solitary life cycle, but it is social in other parts of its known range. The brood is protandrous, with a nearly equal investment in the sexes. Productivity averages 6.5 offspring per foundress female, similar to the second brood of social nests in New York, but less than the combined productivity of both New York broods. *Leucophora* sp. (Diptera: Anthomyiidae) is the principal cause of brood mortality in Colorado. Foundress females in about half the nests survive until brood emerge as adults. Retention of these foundresses decreases offspring mortality by 68%. Comparable abilities to express solitary behavior with a single brood may characterize other eusocial halictine lineages that have successfully invaded high altitudes in the Rocky Mountains. The apparent inability to do this may help explain the absence of other eusocial halictine bees and polistine wasps at high altitudes, despite their success at lower elevations in the same mountains. Presence or absence of this ability may help explain latitudinal distributions of these lineages in North America. Holarctic distributions of lineages with eusocial behavior can be explained by migration as solitary populations from Eurasia to North America across Pleistocene Bering land bridges, with re-expression of double-brooded, eusocial behavior when the species then extended their ranges southward in North America.

**Key words** *Halictus rubicundus* · High-altitude population · Solitary behavior · *Leucophora* · Holarctic distribution

G.C. Eickwort[1] · J.M. Eickwort[2] · J. Gordon[3]
M.A. Eickwort[4]
Rocky Mountain Biological Laboratory, Crested Butte, CO 81224, USA

G.C. Eickwort[1]
Department of Entomology, Cornell University, Ithaca, NY 14853, USA

W.T. Wcislo (✉)
Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002-0948, USA

[1]1940–1994 (see Wcislo WT, 1996) Commentary: Solitary behavior in social bees. Behav Ecol Sociobiol 38:235–236

*Present addresses:*
[2]105 Birchwood Dr., Ithaca, NY 14850, USA

[3]Department of Entomology, Clemson University, Clemson, SC 29634, USA

[4]School of Veterinary Medicine, University of Wisconsin, Madison, WI 53706, USA

## Introduction

Eusocial behavior, with overlap of generations and a worker caste, has traditionally been considered an evolutionary endpoint. Except for social parasites, species which have evolved eusociality were thought to produce descendants which themselves were always eusocial, thus producing the completely social lineages of ants, termites, polistine and vespine wasps, honey bees, bumble bees, and stingless bees (Wilson 1971). Sweat bees (Hymenoptera: Halictidae; Halictinae), however, which have evolved primitive eusociality many times (Michener 1974, 1990), also have the ability to express solitary behavior in eusocial lineages (for reviews, see Michener 1990; Packer 1993; Danforth and Eickwort in press; Wcislo in press; Yanega in press).

In this paper, we describe life-cycle modifications of an eusocial sweat bee, *Halictus rubicundus*, that permit solitary behavior at high altitudes in the New World Rocky Mountains. Similar adaptations may enable diverse lineages of social insects to utilize high-altitude habitats. We suggest that these adaptations have also permitted the invasion of high latitudes and have led to current Holarctic distributions.

Nearly all temperate eusocial halictines, including *H. rubicundus*, have annual colonies and produce at

least two temporally separated broods during each flight season. The first brood consists of many females and some males, and most or all of the females become workers in the natal nest. The second brood consists of males and females that mate, after which females enter diapause and initiate colonies the following year. The flight season is too short at high altitudes and latitudes to permit two broods, so sweat bees that live under such conditions must either be originally solitary, secondarily evolve a solitary life cycle, or possess a developmental system that can facultatively express social or solitary behavior. The discovery of a population of *H. rubicundus* nesting in the subalpine region of Colorado permitted investigation of whether solitary behavior is based on an evolutionary loss of worker behavior, or on facultative expression of different social phenotypes under different conditions. Additionally, we examined whether solitary behavior entails costs such as a lower number of reproductive brood produced per foundress or increased brood mortality.

## Materials and methods

### Natural History

*H.* (*H.*) *rubicundus* is a Holarctic sweat bee, distributed across Eurasia and North America south to Florida, Arizona, and California (Moure and Hurd 1987). It is social at lower elevations in Europe (Knerer 1980), southern Ontario (Knerer 1980), coastal British Columbia (Packer and Owen 1989), Oregon (G.C. Eickwort, unpublished work), Kansas (Yanega 1993), and New York (Yanega 1988). Bonelli (1967) briefly described a solitary population from the mountains of Italy, although sociality cannot be precluded for this population (see Sakagami 1980). The most thorough studies of *H. rubicundus* have been on a New York population, which form the basis of the following summary (Yanega 1988, 1989, 1990).

Inseminated females overwinter away from the nest site, and return in April to individually excavate nests in the soil. Each female constructs and provisions up to 11 female-producing cells and up to 5 male-producing cells over a 1-month period. From the end of provisioning to the emergence of adults takes approximately 2 weeks, during which the foundress remains in her nest, presumably with her ovaries regressed. This first brood is female-biased, and adults begin emerging in mid- to late June. Males leave the nests and mate with some of the emerging females. Most of the earlier-emerging females do not mate ($\geqslant 90\%$), and return to the nests to act as workers. Later-emerging females in the first brood are more likely to mate upon emergence, as males become increasingly abundant; by the 3rd week of emergence, 100% of the emerging females mate. These immediately mated females leave the nest site to enter hibernation and become nest foundresses (gynes) the following spring, while the workers and replacement queens do not diapause, even though eventually over half of them mate. With the emergence of adult workers, the foundress no longer leaves the nest to forage and becomes a queen, and presumably her ovaries again develop. The nest is enlarged and her worker daughters provision up to 25 more cells. Provisioning ends about the middle of July, and a 1-week inactive period ensues until the emergence of adults from the second brood. This second brood averages 42% female, and these females do not work. Both sexes leave the nests and mate, and inseminated females leave the nest site to hibernate. Along with previously hibernating females from the first brood, they will be the foundresses of new colonies the following spring.

### Methods

Studies were conducted at the Rocky Mountain Biological Laboratory (RMBL), in the East River valley of the western slope of the Rocky Mountains, near Gothic, Gunnison County, Colorado, United States, in the summers of 1984 and 1988. RMBL is in the subalpine zone (altitude 2850 m), which is characterized by spruce-fir forests interspersed with meadows. In 1984, only three scattered nests were located in bare patches in disturbed meadows adjoining buildings. These active nests were marked on 3 and 5 July, and excavated on 11 and 17 August. In 1988, a nest aggregation was discovered in bare ground on a footpath along a south-facing slope on 15 June, at the beginning of floral bloom. The site ($2.85 \times 2.30$ m) was immediately roped off to prevent disturbance. Between 16 and 28 June, the site was observed on 8 days for a total of 19 h. By watching returning bees 41 nests were discovered and they were marked with numbered plastic stakes and numbered nails. Many females returning to or leaving nests were netted and marked with Testor's PLA blue enamel paint to identify them as foundresses, then released. By 2 July, nearly all foraging had ceased, and most nest entrances were closed with soil. On 9 July, for 37 nests, the number of neighboring nests within a 30-cm radius was counted. Between 2 and 13 July 28 nests were excavated and 8 nests were excavated between 1 and 3 August; adult bees from the nests were measured and dissected, and mature larvae and pupae were reared in the laboratory, following the methods of Abrams and Eickwort (1980).

Additional observations at the nest aggregation were conducted on 25 July to determine activity of bees in individual nests (1 h). Spot checks were frequently taken to determine whether bees were bringing pollen to nests during July.

Six scattered nests were discovered in hard-packed, bare, level ground near a laboratory building, and were marked on 21–25 June 1988. Three nests from this site were excavated on 14 July, and three nests were excavated on 3 August.

Collecting expeditions were taken on 15 June and 26 July, 1988, down the East River valley to determine the activity of *H. rubicundus* and other species of halictine bees at slightly lower elevations in a riparian environment surrounded by sage meadows (elevation 2400 m) (at Roaring Judy Fish Hatchery, near Almont).

Measurements are expressed as mean ±standard error. Voucher specimens from this study are deposited in the Cornell University Insect Collections, lot number 995.

## Results

### Seasonal phenology

Adult female *H. rubicundus* initiated nests and foraged for pollen and nectar coincident with the first blooming plants at Gothic, while snow still persisted in shaded locations (15 June in 1988). Nests were provisioned whenever weather conditions permitted for the next 8 days. On 25 June, about half of 42 marked nests in the aggregation were closed with soil, and foragers returning with pollen were noted in only eight nests in 1 h of observation. Most of the 28 nests excavated in the period 2–14 July reflected the cessation of reproductive activity in late June, but four nests were still active, containing fresh pollen or eggs. Of the 28 nests 16 still contained foundresses when excavated in July. Only one foundress was found in each of these nests, and observations of nests with marked bees in June gave no indication of the presence of more than one bee in any nest.

The first male was observed in flight on 19 July 1988, just south of Gothic, marking the beginning of emergence of the brood. On 25 July, 9 of 19 marked nests (47%) in the aggregation had open entrances, and some females without pollen were observed entering nests; males were patrolling the site and were also observed patrolling on composites. No females were observed gathering pollen during the latter part of July or early August. Of the 11 nests excavated on 2 and 3 August 6 (54.6%) still contained foundresses, as indicated by worn wings or blue paint (two females). One of the three nests excavated on 11–17 August 1984 also contained the foundress female. The August nests from 1984 and 1988 contained pupae and callow (newly emerged) adults. Cells from which adults had emerged were usually filled with soil and were difficult to distinguish from the substrate. There was no indication that new brood was produced in July or August. Foundresses ($n = 9$) present in nests excavated in August had slender ovaries, with yellow bodies indicating past oviposition. Adult females from this brood did not appear to overwinter in their natal nests, as only callow adults were found in the burrows.

Phenology of other halictines nesting at Gothic followed the above pattern. At the lower elevation of Almont, *H. rubicundus* occurred but it was uncommon, and only a few males were captured on 26 July. However, females of the more abundant *H. confusus* and *Lasioglossum* (*Dialictus*) spp. were collecting pollen at Almont on 26 July, and dissections of five *H. confusus* and four *L.* (*D.*) *pacatus*[1] showed that all had worn mandibles, slender ovaries, and lacked sperm in the spermathecae, which are characteristics of halictine workers.

## Nest productivity and brood sex ratio

Vacated cells were filled with soil and were difficult to locate, so productivity data were based on nests excavated on 2–14 July, before adult emergence (and excluding the three burrows that lacked cells). The productivity of the nests outside the aggregation ($\bar{x} = 6.2 \pm 1.35$ offspring per nest, $n = 5$) was not significantly different from that of nests within the aggregation ($\bar{x} = 6.5 \pm 0.87$ offspring, $n = 23$) ($t = 0.162$, $P > 0.8$, two-tailed). Table 1 presents data on the total number of cells in nests and the number containing viable brood, contrasting nests with and without foundresses at the time of excavation. The four nests whose females were still provisioning cells included the two most productive nests (15 offspring each), but mean productivity of nests with still-active females ($10.5 \pm 2.63$ offspring) was not different from that of the 13 nests containing inactive females ($7.1 \pm 0.70$ offspring) (Mann-Whitney $U = 35.5$, $P = 0.279$).

[1]G.C. Eickwort was uncertain about the identity of this species, and labelled voucher specimens cannot be located (W. Wcislo)

**Table 1** Productivity of nests of *Halictus rubicundus* with and without foundress females present when nests were excavated (2–14 July 1998). Values given are mean ± SEs

| Group ($n$) | Total cells (range) | Number brood | Dead cells[a] | Fly mortality[b] |
|---|---|---|---|---|
| With foundress (17) | 9.8 ± 0.81 (6–18) | 7.9 ± 0.85 | 0.9 ± 0.2 | 0.4 ± 0.17 |
| Without Foundress (11) | 6.4 ± 1.28 (1–13) | 4.3 ± 1.13 | 1.8 ± 0.48 | 0.6 ± 0.36 |
| Total (28) | 8.5 ± 0.76 (1–18) | 6.5 ± 0.75 | 1.3 ± 0.23 | 0.5 ± 0.17 |

[a]Includes moldy cells, and those with evidence of fly predation, but does not include empty cells
[b]Subset of preceding dead cells with known fly predation

Of 39 nests, 9 (23.1%) displayed evidence of *Leucophora* fly predation, 15 nests (38.5%) had moldy cell contents, and 15 nests (38.5%) suffered no mortality due to flies or other causes. A parasitic fly, probably *Phalacrotophora halictorum* (Diptera: Phoridae), was also observed at the site. No evidence of parasitism was recovered during nest excavations, but these flies leave the cell to pupate, and would not be recovered from cells (see Wcislo 1990). In the 28 nests excavated on 2–14 July, 84.2% of the 221 cells contained healthy bee brood, while 7.2% contained flies and 8.6% had moldy contents. On a *per capita* basis, the proportion of destroyed cells for nests within the aggregation ($\bar{x} = 0.29 \pm 0.06$, $n = 23$) was different from those outside the aggregation ($\bar{x} = 0.077 \pm 0.06$, $n = 5$) (Mann-Whitney $U = 25$, $P = 0.057$). Mortality attributable to flies was restricted to nests within the aggregation, although sample sizes were small. The presence of a foundress female in a nest influenced offspring mortality (Table 1). The proportion of unsuccessful cells per nest when an adult was present at the time of excavation ($\bar{x} = 0.15 \pm 0.042$, $n = 17$) was less that observed in nests without an adult female ($\bar{x} = 0.44 \pm 0.12$, $n = 11$) (Mann-Whitney $U = 56$, $P = 0.07$) (Table 1).

The Gothic population of *H. rubicundus* was protandrous in 1988. The male:female sex ratio of callow adults, pupae, and larvae that could be reared to pupae from nests excavated on 2-14 July was 2.13, while the comparable sex ratio from nests excavated on 1–3 August was 0.86 (Table 2). The overall male:female ratio was 1.72, based on all the nests excavated throughout 1988. However, this estimate does not take into account the fact that July nests contained 49 brood whose sex could not be determined because they were too young, and August nests consisted mostly of vacated cells. Assuming that the observed sex ratios apply to the unsexed brood of the same age cohort, the corrected overall sex ratio was 1.68, based on all brood in the July nests. An investment ratio (based on the

**Table 2** Sex ratio of brood of *H. rubicundus* in nests excavated at the beginning and the end of adult emergence in 1988 in Gothic, Colorado

| Date excavated (*n*) | Number females | Number males | Male:female ratio |
|---|---|---|---|
| All nests (37) | 67 | 115 | 1.72 |
| 2–14 July (26) | 45 | 96 | 2.13 |
| 2–3 August (11) | 22 | 19 | 0.86 |
| 2–14 July, adjusted[a] (26) | 71 | 119 | 1.68 |

[a]Includes 49 cells before pupation, multiplied by 0.54 female equivalents (2–3 August)

corrected sex ratio) of 1.11 (male:female) was estimated by taking into consideration the fact that 1 male = 0.66 female by weight (G.C. Eickwort, unpublished work); in another halictine bee (*H. ligatus*) metabolism of male and female brood apparently does not differ (Boomsma and Eickwort 1993). There was no significant difference in size, based on head width, between foundresses ($\bar{x} = 7.2 \pm 0.08$ mm, $n = 21$) and reared female brood ($\bar{x} = 7.1 \pm 0.3$ mm, $n = 4$) (Mann-Whitney $U = 42.5$, $P > 0.9$).

## Discussion

### Structure of the single brood and loss of worker behavior

Though eusocial elsewhere, *H. rubicundus* is a single-brooded, solitary bee at Gothic. The absence of foraging females and new cell construction in August, just before the end of the growing season, indicated that only one brood was produced. The equivalent size of nest-making females and their female brood is additional evidence that no workers were produced. This is similar to the situation in *Lasioglossum* (*Evylaeus*) *calceatum* in Hokkaido, Japan, in which a solitary population exists at high altitudes (1167 m) and eusocial populations exist at low altitudes (150–200 m) (Sakagami and Munakata 1972). Our findings lend credence to the report of Bonelli (1967) of a solitary high-altitude population of *H. rubicundus* in Italy.

Due to the short flight season, the emerging brood of the Gothic population would not have time to produce a second brood, environmentally precluding a "worker" generation. The protandrous, male-biased single brood of the Gothic population is more similar to the second (reproductive) brood of eusocial populations (Yanega 1989), than to the first (worker) brood. Worker behavior could be lost via deletion of the worker brood, but information on brood structure cannot exclude either the hypothesis that social behavior has been evolutionarily lost, or is facultatively suppressed. Sex ratios in halictine bees can change under different abiotic and social conditions (Mueller 1991). For example, Plateaux-Quénu and Plateaux (1980) reared foundresses from a single population of *L.* (*E.*) *calceatum* at different temperatures, and found that under cooler temperatures the first brood contained 47% males, compared with 17% under warmer temperatures (for review, see Yanega in press). Yanega (1989) hypothesized for *H. rubicundus* that caste is determined by mating status within a critical period shortly after emergence. If true, then an environmentally-induced shift in the sex ratio, like that reported for *L.* (*E.*) *calceatum*, would result in a higher frequency of mated females, and leave a negligible pool of females in the worker caste.

Nesting activity in Gothic begins at about the same time of the year as the beginning of the second brood (diapause offspring) elsewhere. This observation may suggest a common behavioral mechanism for the lack of worker behavior, and support the contention of Yanega (1989) that working is an alternative behavior expressed when diapause is precluded. Adult bees of another basically solitary bee, *Ceratina japonica*, that are in reproductive diapause do not work, but diapause can be terminated by cooling or topical application of juvenile hormone (Maeta et al. 1993). Experimental studies are needed for halictines in general, and *H. rubicundus* in particular, to address what factors induce diapause, and ascertain which factors regulate the switch in behavior between females of non-reproductive and reproductive broods.

### Mortality and productivity at high altitudes

The principal mortality factor for *H. rubicundus* at Gothic was fly predation, especially by satellite flies (*Leucophora* sp.) (see Meyer-Holzapfel 1986). When nests were constructed within 30 cm of each other, the resulting aggregation appeared to concentrate the patrolling activities of the flies, and brood mortality was significantly greater than for nests that were more widely separated (for discussion, see Rosenheim 1990). Overall productivity of isolated nests was not significantly different from that of aggregated nests, suggesting that there may be ameliorating factors in favor of gregarious nesting behavior (see Wcislo 1984). Since isolated nests were difficult for us to locate, our sample size was small, and any conclusions in this regard are tentative.

Of more interest is that the presence of a foundress female in the nest up to the emergence of her brood resulted in a three-fold decrease in mortality, both overall mortality and that due to flies. There is thus a considerable selective advantage for a female in living long enough to overlap with the emergence of her adult offspring, even in this functionally solitary population. This important characteristic of eusociality (*sensu* Michener 1974) thus could function as an exaptation for derived solitary existence.

The mean productivity of the Gothic population (6.5 brood/nest for nests within the aggregation) is similar to the second brood in the New York population (5.7 brood/nest, Yanega 1989). This observation suggests that, at the limits of its altitudinal range, *H. rubicundus* is well-adapted as a solitary bee. Our impression is that *H. rubicundus* is more abundant at Gothic as a solitary bee, than at lower elevations where it could be social and produce two broods.

## Ability of other social insects to adapt to high altitudes

From the example given by *H. rubicundus*, it is apparent that social insects capable of adapting to high altitudes would have an expanded range in which populations could flourish in the rich resources which are available over a short season. *H. rubicundus* may not be the only social halictine bee that is solitary at high altitudes in the Rocky Mountains. *L. (D.) pacatus* is eusocial at lower elevations but is probably solitary in Gothic (G.C. Eickwort, unpublished work). Other halictine species present at lower elevations (e.g., *Augochlorella pomoniella* and *H. ligatus*) show no indication of being able to exist as solitary populations in the high mountains, nor are there species there that might be their descendants.

Similar considerations exist for other groups of social insects. Paper wasps (Vespidae: Polistinae) are represented in Almont by eusocial *Polistes* and *Mischocyttarus*. These show no ability to exist as single-brooded solitary populations, and both genera are absent from Gothic. In contrast, yellowjackets and hornets (Vespidae: Vespinae) are present in both Almont and Gothic. They maintain their eusocial status at high altitudes by fitting two broods into the short summer. They are able to do this because of their ability to thermoregulate and warm their brood. A similar thermoregulatory ability explains the success of eusocial bumble bees (*Bombus*, Apidae) at Gothic and other subalpine and alpine habitats (see Heinrich 1979).

Perennial eusocial insects adapt to high altitudes only by successfully overwintering as intact colonies (e.g., many ant taxa). Honey bees (*Apis mellifera*, Apidae) are successful in Almont, but cannot survive in Gothic. The growing season at Gothic appears to be too short for them to store enough honey to maintain a colony over the winter (O.R. Taylor, personal communication).

## Ability of social insects to adapt to high latitudes

High latitudes, like high altitudes, are characterized by growing seasons that are too short for two generations of most social insects. Nevertheless, the range of *H. rubicundus* extends into the boreal regions of Ontario, Canada (Knerer and Atwood 1962), and Alaska (Armbruster and Guinn 1989). While no studies of nesting populations have been conducted in these areas, seasonal phenology indicates that these populations and those of other halictines in the same areas are solitary (Armbruster and Guinn 1989). Indeed, the furthest north that halictines are known to exist as social populations is near Calgary (~52°N) (e.g., Packer and Owen 1989).

Of the 18 non-parasitic, presumably solitary, halictine species recorded from boreal Ontario by Knerer and Atwood (1962), 7 (39%) are known to be eusocial in New York (*H. rubicundus*, *H. confusus*, *L. (Evylaeus) truncatus*, *L. (Dialictus) laevissimum*, *L. (D.) nigroviridis*, *L. (D.) rohweri*, and *L. (D.) pilosum*)[2]. These lineages have been able to greatly extend their range northward in contrast to such otherwise successful eusocial species in New York and southern Canada as *H. ligatus*, *L. (E.) cinctipes*, *L. (D.) zephyrum*, *L. (D.) lineatulum*, *L. (D.) imitatum*, and *Augochlorella striata*[2]. We hypothesize that these latter species have been unable to survive as solitary populations, and thus are limited to locations where two broods per year are always possible. This also holds true for other social insect taxa. The obligatorily eusocial polistine wasps are limited to those portions of Canada below the boreal forest (Starr 1991). Honey bees and termites are excluded from the boreal region as they are from high altitudes, while bumble bees, vespine wasps, and various groups of ants are as capable of colonizing high latitudes as they are high altitudes.

Those eusocial lineages that express solitary behavior at high latitudes also were potentially able to take advantage of the Bering land bridge between Siberia and Alaska in the Pleistocene. At that time the climate was essentially boreal, with short summers (Lozhkin et al. 1993), although the land bridge itself was a steppe prairie that supported numerous flowers (Matthews 1980). According to Pesenko (1984), all the close relatives of *H. rubicundus* are Old World species. We suggest that the presently holarctic species *H. rubicundus* crossed the bridge from Asia to North America in the Pleistocene as solitary bees, having been eusocial elsewhere in Asia (also Michener 1990). As these populations moved southward in North America, they encountered warmer climates and eusociality was again expressed where it was possible to have two broods in a season. Eusocial halictine lineages in both the Old World and the New World that were unable to become solitary never reached the Bering land bridge, and consequently are presently restricted to their continent of origin. The holarctic distributions of species of vespine wasps, bumble bees, and ants can be explained by their ability to adapt to the conditions of the Bering land bridge. The fact that other groups of social insects

[2]Evidence for this statement is based on unpublished notes by G.C. Eickwort, which are with W. Wcislo (see Commentary)

do occur in both the Old and New Worlds, although significantly without holarctic species or species groups, can be explained by migration across much earlier land bridges, perhaps 55 million years ago when conditions were subtropical or tropical in the Eocene (Matthews 1980).

## The evolutionary significance of social flexibility

It has become increasingly evident that the great success enjoyed by sweat bees has in part been due to the flexibility of their primitive eusociality, which permits different expressions under different climatic regimes (for reviews, see Michener 1990; Wcislo in press; Danforth and Eickwort in press; Yanega in press). Those eusocial species that have been able to revert to, or facultatively express, solitary behavior have been able to invade subalpine and boreal habitats and even to cross between continents. Phylogenetic analyses of some *Halictus* (Richards 1994) and of some *Lasioglossum* (*Evylaeus*) species (Packer 1991) have indicated that eusociality may be the ancestral condition in both these sweat bee taxa, with independent reversions to solitary nesting. As Michener (1990) has recently emphasized, the old question of how many times eusociality has evolved in insects may become impossible to answer within the Halictidae. If *H. rubicundus* was originally eusocial in Asia, then evolved a solitary population that crossed the Bering Land Bridge into Alaska in the Pleistocene, and later re-evolved eusociality in southern Canada, is this one or two origins of eusociality? Transplant and common garden experiments with bees like *H. rubicundus* will help answer this important question.

**Acknowledgements** We are grateful to the Rocky Mountain Biological Laboratory for allowing us to close off a pedestrian pathway in order to preserve the nest aggregation, and for providing facilities for this study. We thank U. Mueller for statistical advice, and L. Packer and W. Wcislo for comments on the manuscript (incorporated by W. Wcislo into the revised version).

## References

Abrams J, Eickwort GC (1980) Biology of the communal sweat bee *Agapostemon virescens* (Hymenoptera: Halictidae) in New York State. Search: Agric Cornell Univ Agric Exp Sta 1:1–20

Armbruster WS, Guinn DA (1989) The solitary bee fauna (Hymenoptera: Apoidea) of interior and arctic Alaska: flower associations, habitat use, and phenology. J Kans Entomol Soc 62:468–483

Bonelli B (1967) Osservazioni biologiche sugli imenotteri melliferi e predatori della Val di Fiemme [XXIII contributo *Halictus rubicundus* Christ (Hymenoptera-Halictidae)]. Stud Trentini Sci Nat Sez B 44:85–96

Boomsma JJ, Eickwort GC (1993) Colony structure, provisioning, and sex allocation in the sweat bee *Halictus ligatus* (Hymenoptera: Halictidae). Biol J Linn Soc 48:355–377

Danforth BN, Eickwort GC (in press). The evolution of social behavior in the augochlorine sweat bees (Hymenoptera: Halictidae) based on a phylogenetic analysis of the genera. In: Crespi B, Choe J (eds) Social competition and cooperation in insects and arachnids, vol 2. Evolution of sociality. Cambridge University Press, Cambridge

Heinrich B (1979) Bumblebee economics. Harvard University Press, Cambridge

Knerer G (1980) Biologie und Sozialverhalten von Bienenarten der Gattung *Halictus* Latreille (Hymenoptera; Halictidae). Zool Jb Syst 107:511–536

Knerer G, Atwood CE (1962) An annotated check list of the non-parasitic Halictidae (Hymenoptera) of Ontario. Proc Entomol Soc Ont 92:160–176

Lozhkin AV, Anderson PM, Eisner WR, Ravoka LG, Hopkins DM, Brubaker LB, Colinvaux PA, Miller MC (1993) Late Quaternary lacustrine pollen records from southwestern Beringia. Quart Res 39:314–324

Maeta Y, Saito K, Hyodo K, Sakagami SF (1993) Diapause and non-delayed eusociality in a univoltine and basically solitary bee, *Ceratina japonica* (Hymenoptera, Anthophoridae) I. Diapause termination by cooling and application of juvenile hormone analog. Jpn J Entomol 61:203–211

Matthews JV Jr (1980) Tertiary land bridges and their climate: backdrop for development of the present Canadian insect fauna. Can Entomol 112:1089–1103

Mueller U (1991) Haplodiploidy and the evolution of facultative sex ratios in a primitively eusocial bee. Science 254:442–444

Meyer-Holzapfel M (1986) Vergleichende Betrachtung des Verhaltens brutparasitischer Fliegen aus zwei Familien bei solitären Aculeaten Hymenopteren. Bull Soc Entomol Suisse 59: 95–110

Michener CD (1974) The social behavior of the bees. Harvard University Press, Cambridge

Michener CD (1990) Reproduction and castes in social halictine bees. In: Engels W (ed) Social insects: an evolutionary approach to castes and reproduction. Springer, Berlin Heidelberg New York, pp 75–119

Moure JS, Hurd PD Jr (1987) An annotated catalog of the halictid bees of the Western Hemisphere (Hymenoptera: Halictidae). Smithsonian Institution Press, Washington

Packer L (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

Packer L (1993) Multiple-foundress associations in sweat bees. In: Keller L (ed) Queen number and sociality in insects. Oxford University Press, Oxford, pp 215–233

Packer L, Jessome V, Lockerbie C, 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

Packer L, Owen RE (1989) Allozyme variation in *Halictus rubicundus* (Christ): a primitively social halictine bee (Hymenoptera: Halictidae). Can Entomol 121:1049–1057

Packer L, Owen RE (1989) Notes on the biology of *Lasioglossum* (*Evylaeus*) *cooleyi* (Crawford), an eusocial halictine bee. Can Entomol 121:431–438

Pesenko YA (1984) The bees of the genus *Halictus* Latreille sensu stricto (Hymenoptera, Halictidae) of Mongolia and north-western China, with a review of publications on Halictini of this region with a revision of the subgenus *Prohalictus* of the world fauna (in Russian). In: Korotyaev BA (ed) Insects of Mongolia, no 9. Nauka, Leningrad, pp 446–481

Plateaux-Quénu C, Plateaux L (1980) Action de la température sur la taille, la sexe et le cycle des individus de premiere couvée (1) chez *Evylaeus calceatus* (Scop.) (*Hym. Halictinae*): premiere étude expérimentale. Ann Sci Nat 14:27–33

Richards MH (1994) Social evolution in the genus *Halictus*: a phylogenetic approach. Insectes Soc 41:315–325.

Rosenheim JA (1990) Density dependent parasitism and the evolution of aggregated nesting in the solitary Hymenoptera. Ann Entomol Soc Am 83:277–286

Sakagami SF (1980) Bionomics of the halictine bees in northern Japan. 1. *Halictus* (*Halictus*) *tsingtouensis* (Hymenoptera, Halictidae), with notes on the number of origins of eusociality. Kontyû 48:526–536

Sakagami SF, Munakata M (1972) Distribution and bionomics of a transpalaearctic 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

Starr CK (1991) *Polistes* distribution. Sphecos 21:5

Wcislo WT (1984) Gregarious nesting of a digger wasp as a "selfish herd" response to a parasitic fly (Hymenoptera: Sphecidae; Diptera: Sacrophagidae [sic]). Behav Ecol Sociobiol 15:157–160

Wcislo WT (1990) Parasitic and courtship behavior of *Phalacrotophora halictorum* (Diptera: Phoridae) at a nesting site of *Lasioglossum figueresi* (Hymenoptera: Halictidae). Rev Biol Trop 38:205–209

Wcislo WT (in press) Behavioral environments of sweat bees (Halictinae) and variability in social organization. In: Crespi B, Choe J (eds) Social competition and cooperation in insects and arachnids, vol 2. Evolution of sociality. Cambridge University Press, Cambridge

Wilson EO (1971) The insect societies. Harvard University Press, Cambridge

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 (1990) Philopatry and nest founding in a primitively social bee, *Halictus rubicundus*. Behav Ecol Sociobiol 27:37–42

Yanega D (1993) Environmental influences on male production and social structure in *Halictus rubicundus* (Hymenoptera: Halictidae). Insectes Soc 40:169–180

Yanega D (in press) Demography and sociality in halictine bees (Hymenoptera: Halictidae). In: Crespi B, Choe J (eds) Social competition and cooperation in insects and arachnids, vol 2. Evolution of sociality. Cambridge University Press, Cambridge

Communicated by P. Pamilo