

**The Nesting Biology of the Sweat Bee *Halictus farinosus* in
California, with Notes on *H. ligatus*
(Hymenoptera: Halictidae)**

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The state of California has long been an important location for research in wild bees, yet until now there have been no studies there on the nesting biology of primitively eusocial bees. Such bees do occur in California, in the genera *Halictus*, *Dialictus*, and *Evylaeus* of the Halictinae. This paper presents information on the nesting behavior of *Halictus (Halictus) farinosus* for the first half of its seasonal cycle in Davis, California, with some notes on *H. (H.) ligatus*.

The range of *H. farinosus* (Fig. 2) extends from Montana, Nebraska, and New Mexico west to British Columbia and California (Moldenke and Neff, 1974; Moure and Hurd, 1984). It is one of the largest and most common sweat bees in California, occurring throughout the state except in the deserts and high mountains. It can be readily distinguished from the three other North American species of the subgenus *Halictus* (two of which occur in California) by the keys in Sandhouse (1941) and Roberts (1973). It builds conspicuous nests in the soil and is in flight from mid February to mid September in California (Moldenke and Neff, 1974). *Halictus farinosus* is broadly polylectic, with collection records from 101 genera of plants (Nye, 1980; Moure and Hurd, 1984). When locally abundant, it can be an important pollinator of crops such as sunflower, *Helianthus annuus* (Parker, 1981), and onion, *Allium cepa* (Parker, 1982 and references therein).

Surprisingly, until 1980 only scattered reports on the nesting biology of *H. farinosus* had been published. A drawing of a nest appeared in Bohart (1952), and Stephen et al. (1969) presented scattered notes on the nest entrance, cell depth and structure, nest guarding, nest establishment in the spring, and generation overlap, presumably based on studies in Utah. These were nicely summarized by Roberts (1973), who correctly inferred that the species is primitively eusocial. Knerer (1980), in contrast, assumed that *H. farinosus* is solitary. In 1980, W. P. Nye published a well-illustrated report of the nesting biology of *H. farinosus* in Utah, including seasonal cycle, flowers visited, foraging behavior, nest site characteristics, nest architecture, development of immatures, and predators and parasites. However, Nye presented few quantitative data and did not dissect or measure nest inhabitants, and consequently gave little information on caste structure. In this paper I describe the rather different spring and early summer colony structure in Davis, California, analyze the castes in second generation nests, and present additional data on nest structure and predators,inquilines, and usurpers.

Halictus ligatus dug loosely aggregated nests near an *H. farinosus* nest aggregation in Davis. In contrast to *H. farinosus*, *H. ligatus* has been the subject of numerous excellent biological studies, particularly those of Chandler (1955) in Indiana, Litte (1977) in New York, Knerer (1980 and earlier papers) in Ontario,

Michener and Bennett (1977) in Trinidad, and Packer (in progress, pers. comm.) in Florida. Michener and Bennett (1977) presented an analysis of geographical variation in nesting biology and social organization of this widespread species, whose range extends coast to coast, from Canada to Venezuela. I present my few data to extend our knowledge of *H. ligatus* social structure to California.

MATERIALS AND METHODS

Field studies were conducted in Davis, Yolo County, California, from 14 April to 25 June 1979. Most observations and all excavations of *H. farinosus* were made at two nest aggregations (sites 1 and 2) along the banks of Putah Creek on the University of California campus. Brief observations were conducted at a third aggregation (site 3) in a suburban yard. Nest excavations and examination, preservation, and rearing of cell contents followed the procedures outlined in Abrams and Eickwort (1980). Useful data were obtained from 11 nests, containing a total of 30 adult female bees and 174 cells, excavated on 25 April (1 nest), 17 May (5 nests), 4 June (1 nest), 14 June (2 nests), and 25 June (2 nests) (Table 1; nests excavated 25 June from site 2, others from site 1). Dissections of adult females also followed Abrams and Eickwort (1980), with the additional measurement of maximum width of one ovary with an ocular scale fitted to a stereomicroscope.

Nests of *Halictus ligatus* were loosely aggregated along the banks of Putah Creek. Three nests, containing a total of 29 cells and one female each, were excavated on 21 May using the same procedures as for *H. farinosus*.

Voucher specimens are deposited in the Cornell University Insect Collections, lot number 995. Data were analyzed using Student's *t*-test and Pearson product-moment correlation, with significance levels of $P < 0.05$.

RESULTS

Halictus farinosus

Seasonal cycle.—*Halictus farinosus* were first observed flying at nest aggregation 1 on 14 April, when nests had conspicuous tumuli and females were bringing in pollen. Obviously nesting activity was well underway. In Utah, females do not overwinter in the nest site. They emerge from early or mid April to early or late May and typically return to an old nest site where they dig new burrows. They remain in these for 2–3 weeks before provisioning the first brood cells in late May or early June (Nye, 1980). (Hereafter, references to the Utah population are from Nye, 1980, unless otherwise cited.) The seasonal cycle thus starts earlier in central California. My excavations indicated that the spring nests were also new in California, not reused from the previous year.

Foraging in Davis continued actively until at least 17 May. A nest site was next visited on 25 May, when flight activity was considerably reduced, with few females bringing in pollen. Nest entrances were open, and some had fresh tumuli. On 30 May and 1 June, females at the same site (1) were again very active; many bees were collecting pollen and numerous spring nests had fresh tumuli. A nest excavated on 4 June indicated that this burst of activity marked the emergence of adults from the first (spring) generation and the beginning of a second (summer) generation of cells. A period of relative inactivity appeared to occur between the two generations, in which females did occasionally fly, although few or no cells

were constructed in most nests. Nye does not mention an inactive period in Utah, but the small number of cells (see nest structure and contents) implies that such a period exists. Utah foundress (spring) nests produce only females, while some males were produced in the California foundress nests. Three of 20 pupae in my nests were males, but the sex ratio could not be estimated accurately because contents of younger cells could not be sexed.

Active foraging for the second generation nests in Davis continued until 14 June. When site 1 was again visited on 22 June, foraging activity appeared lower. Two nests excavated on 25 June yielded no eggs but did contain larvae and numerous pupae, some nearly ready to emerge as adults. The sex ratio of these pupae was 12 males to 21 females. A few pollen-collecting foragers were in flight. Consequently there also appeared to be a period of relative inactivity at the end of the second generation, in which only a few foraging females continued to fly. During June, the males that emerged from the foundress nests patrolled nearby flowering shrubs and trees but did not patrol the nests. In Utah, provisioning of second generation nests begins in late June or early July and continues until early or mid August. No males are in flight during this period in Utah.

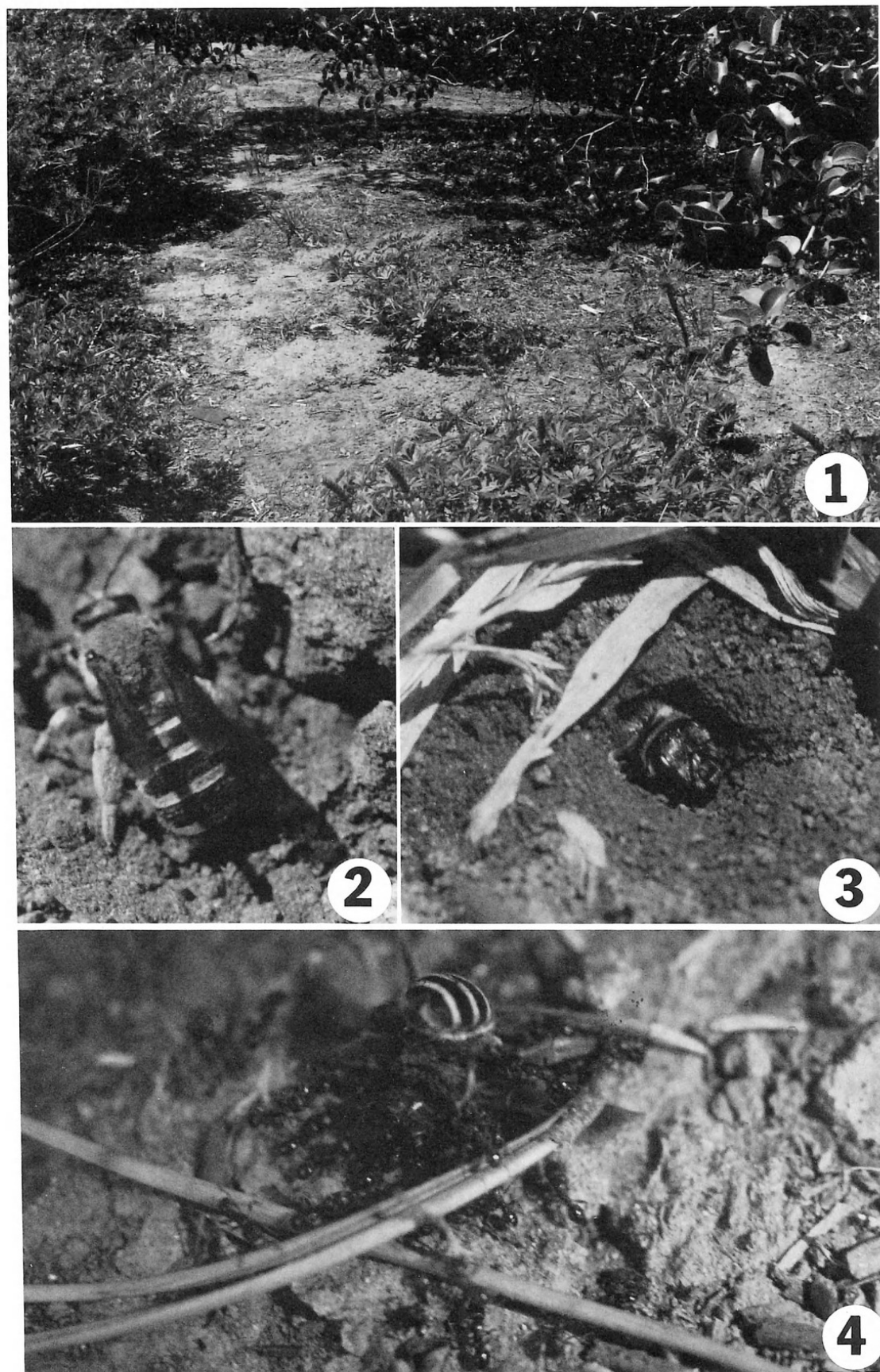
Unfortunately, I had to leave California at the end of June, and thus I could not continue observations of *H. farinosus*. The long flight period reported by Moldenke and Neff (1974) suggests that the sites should have remained active through the rest of the summer, and at least one more generation should have been produced. In Utah the second generation nests produce males and overwintering females (gynes) that first emerge in late July or early August and fly until late September or early October but make no new cells.

Nest sites.—The two Putah Creek nest aggregations were located in dry, nearly level, volcanic silt. Nest entrances were exposed and conspicuous in bare areas of soil, near blooming lupines in site 1 (Fig. 1) and near patches of dry grass in site 2. Nests were excavated from site 1 from 25 April to 14 June and from site 2 on 25 June (Table 1). Site 1 also contained a nest of *Agapostemon texanus* (Halictidae) (described in Eickwort, 1981), and the halictines *Dialictus brunnei-ventris* and *Halictus (Seladonia) tripartitus* nested nearby. Site 2 contained numerous nests of the eumenine wasp *Euodynerus annulatus sulphureus*, and *Halictus ligatus* nested nearby. No isolated nests of *H. farinosus* were located along Putah Creek.

The third Davis site consisted of three contiguous suburban yards, where the conspicuous nests occurred in bare areas of level soil. In one yard these bare areas occurred among low juniper bushes, while in the others they were in mowed grassy lawns. Nests were densely aggregated in two of these yards but were widely scattered in the third.

Nests were also located at Bodega Bay Marine Research Station, Sonoma County, California, on 12 May 1979. These occurred on a high bluff above the Pacific Ocean, in bare areas of level, stabilized and hard-packed sand. The conspicuous nests were scattered or in small aggregations.

In Utah, nests are located in canyons, grassy and brushy slopes, and open woodlands. Nests are preferentially established in dry, compact, well-drained soil, in areas of low, sparse vegetation. Road edges, trails, and trampled or partially denuded areas are preferred, where nests may be aggregated or isolated. Nest site characteristics thus are similar in California and Utah.



Figures 1-4. 1, Nest site 1 of *Halictus farinosus*, Putah Creek, Davis, California. 2, *H. farinosus* female. 3, *H. farinosus* female at nest entrance. 4, Ants (*Tetramorium caespitum*) dragging female *H. farinosus* during raid of nest site 3.

Nest structure and contents.—Nest entrances in Davis were surrounded by conspicuous tumuli, maximum diameters 10.5–14.5 cm ($\bar{x}$ = 12.1 cm, SD = 1.51, n = 7 nests, 14 June). The entrance was asymmetrically placed, 1.5–3.0 cm ($\bar{x}$ = 2.4 cm, SD = 0.61, n = 7) from the nearest edge of the tumulus (Fig. 3). Where undisturbed, the entrance slanted towards the center of the tumulus, which partially covered it from above. A shallow groove in the tumulus, from the entrance to its nearest edge, was sometimes observed. No turret was apparent when the tumulus was brushed away, and the entrance was not conspicuously modified and only slightly narrowed (diameter range 6.5–7.5 mm, $\bar{x}$ = 6.93 mm, SD = 0.354, n = 8 nests, 14 June). The burrow was either directed subhorizontally a short distance towards the center of the tumulus (Fig. 6) before becoming vertical, or it became vertical immediately below the loose tumulus (Fig. 7). Similar tumuli are illustrated for Utah *H. farinosus* by Stephen et al. (1969) and Nye (1980), although they describe a turret within the tumulus that was not apparent in the California nests.

Burrows extended vertically or subvertically to their deepest points. All spring (first generation) nests and most summer (second generation) nests were unbranched; one large summer nest (Fig. 7, no. 10) had one cell-containing branch. Spring nests extended 14–31 cm deep (Fig. 5), while summer nests enlarged from spring nests extended 63–80 cm deep (Figs. 6–7, Table 1). One summer nest (no. 11), apparently newly initiated in June, reached a depth of 32 cm. The burrow diameter of a spring nest (no. 1) excavated on 25 April was 9.0–10.0 mm, comparable to those made by overwintering queens in Utah. Summer nest burrow diameters, however, were 7.0–9.0 mm ($\bar{x}$ = 7.9 mm, SD = 0.46, n = 15).

Cells sloped downwards 9°–21° ($\bar{x}$ = 16°, n = 6) from the horizontal, and were typically halictine in their shape and in possessing a wax-like lining. Spring cells were 12.5–16.0 mm long ($\bar{x}$ = 14.6 mm, SD = 1.48, n = 5) by 6.2–8.0 mm maximum width ($\bar{x}$ = 7.25 mm, SD = 0.715, n = 6), smaller than those reported from Utah. They were joined to the burrows by short laterals, 2.5–4.0 mm long ($\bar{x}$ = 3.13 mm, SD = 0.629, n = 4), that were filled with soil after oviposition. Cells extended in all directions from the burrow and were not surrounded by branch burrows or cavities, and a blind burrow (length 2.0–18.0 cm, $\bar{x}$ = 9.14 cm, SD = 5.056, n = 7) extended below the deepest cells. In spring nests the top cells were 7.5–11.5 cm ($\bar{x}$ = 9.6 cm, SD = 2.12, n = 7) from the soil surface, and the bottom cells were 10.0–23.0 cm deep ($\bar{x}$ = 15.4 cm, SD = 4.33, n = 7). Top cells in reused summer nests were 28–51 cm deep ($\bar{x}$ = 39.0 cm, SD = 11.53, n = 3), below the level of the spring cells which were filled with soil, and bottom cells were 52–75 cm deep ($\bar{x}$ = 65.7 cm, SD = 12.10, n = 3). The single apparently newly initiated summer nest (no. 11) had its top cell 23 cm and bottom cell 30 cm deep. In general, cells containing older instars were above those more recently completed in both spring and summer nests.

Provision masses ranged continuously from small and subspherical in top view

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Figures 5–7. Nests of *Halictus farinosus* in Davis, California, in 1979. 5, Early foundress nest (no. 1) excavated 25 April. 6, Early second-generation nest (no. 7) excavated 4 June. 7, Late second-generation nest (no. 10) excavated 25 June. Cell contents: d, dead (moldy contents); e, egg; l, feeding larva; m, mature (postfeeding) larva; o, pollen only; p, pupa.

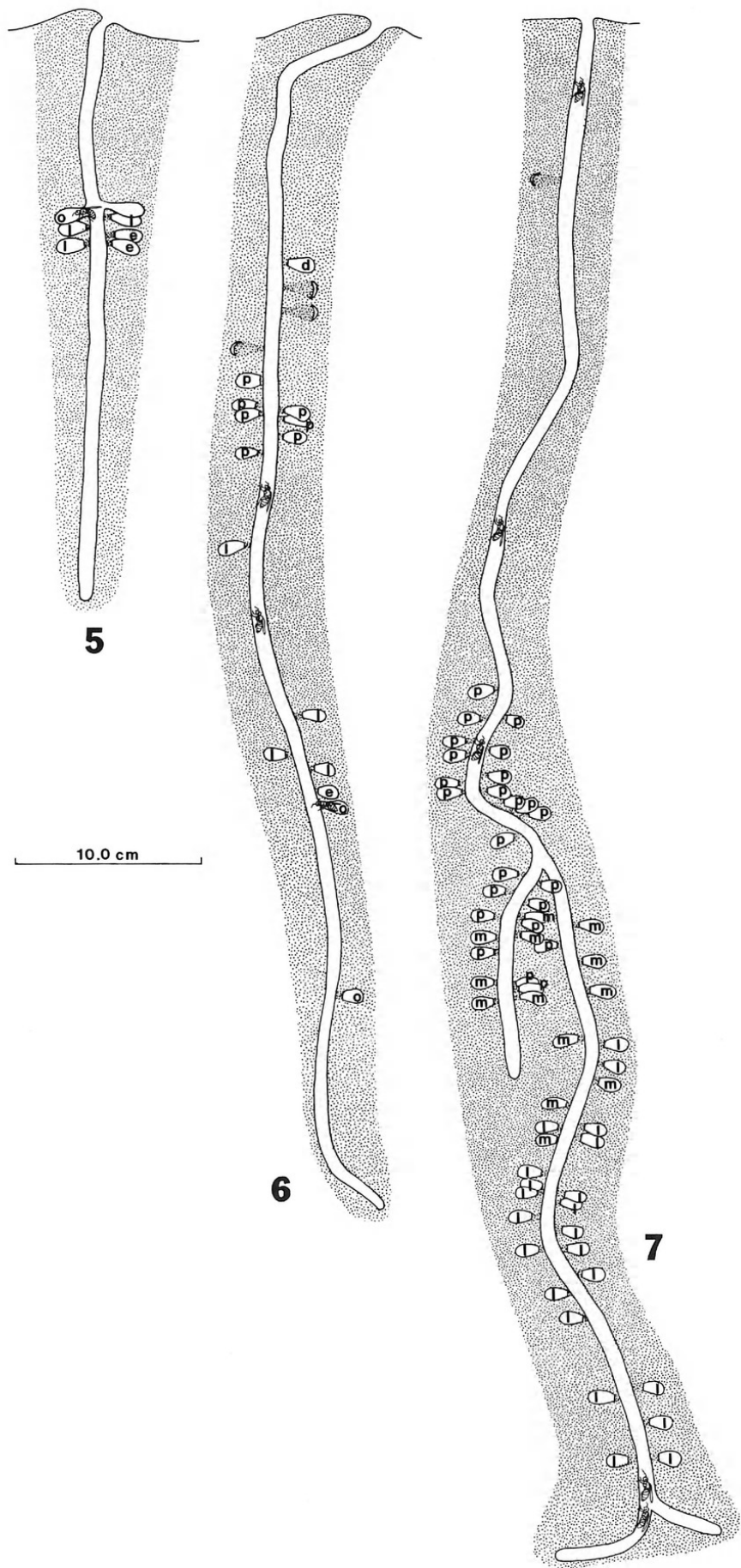


Table 1. *Halictus farinosus* nest contents, 1979.

Nest no.	Date excavated	No. females	No. cells	Burrow depth (cm)
1	25 April	1	7	31
2	17 May	1	11	29
3	17 May	1	9	22
4	17 May	1	4	14
5	17 May	1	25	18
6	17 May	1	11	23
7	4 June	4*	15**	63
8	14 June	6	17	78
9	14 June	2	7	—
10	25 June	10*	59	80
11	25 June	1	9	32

* Including one female that escaped.

** Including eight cells from the first generation.

(length 5.8 mm) to large and subrectangular in top view (maximum length 8.1 mm), with widths of 5.6–7.1 mm ($n = 4$) and heights of 3.8–5.0 mm ($n = 3$). Eggs, larvae and pupae developed like those of other halictines and as illustrated by Nye (1980), although Nye recorded only the smaller spherical provision masses.

The number of cells in each nest is given in Table 1. Most nests were excavated while they were still being provisioned, making an accurate estimate of the number of cells in each generation impossible. The completed spring cell portion of nest no. 7 (Fig. 6) contained 8 cells with pupae plus at least 3 recently abandoned cells, while 4 nests excavated on 17 May, perhaps one week before the end of the spring foraging period, contained 4–11 cells. A fifth nest (no. 5) excavated on that date contained 25 cells; while only one adult female was captured in it, I cannot preclude the possibility that there had been multiple foundresses. One summer nest (Fig. 7, no. 10) excavated on 25 June contained no eggs, thus suggesting that provisioning for the second generation was completed; it had 59 cells. An apparently new summer nest with one adult bee and no eggs excavated on that date (no. 11) had 9 cells.

Utah nests resemble those in California in their basic structure, with the minor differences noted above. However, they differ greatly in the number of cells: Utah first generation nests contain 2–5 cells, in contrast to the 11 or more cells that appear typical of the California population. Second generation Utah nests contain an average of 17 cells (a maximum of 27 cells, including 5 that appear to be first generation soil-filled cells, is illustrated by Nye for one nest from 16 August), while the average was undoubtedly greater for the California nests.

Caste structure.—All excavated spring nests (Table 1) yielded one female bee each, although one or more inhabitants may have been absent from some nests when I began excavations. Utah foundress nests are haplometrotic. The Davis foundresses were all inseminated, all had at least one developed oocyte in their ovaries (ovarian width $\bar{x} = 0.972$ mm, $SD = 0.166$, $n = 5$), all had worn mandibles, and five of six had nicked or tattered wing margins. Mean wing length was 9.00 mm ($SD = 0.307$, $n = 6$) and mean head width was 3.25 mm ($SD = 0.074$, $n = 6$).

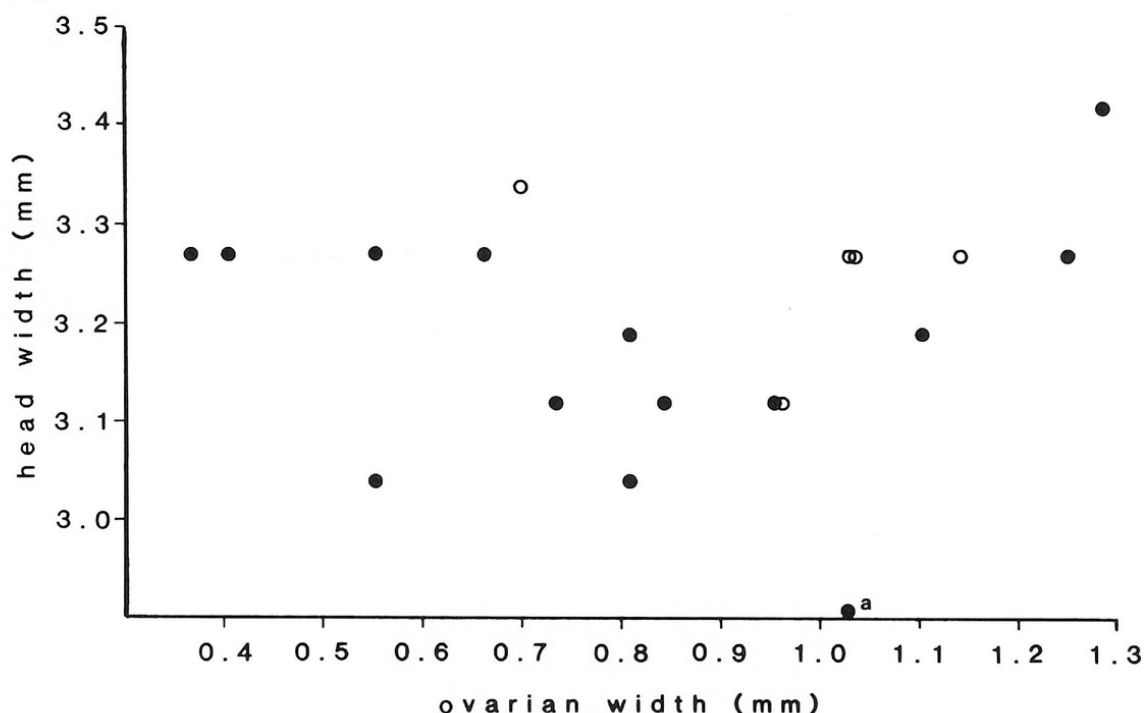


Figure 8. Ovarian width compared with head width, *Halictus farinosus*. Closed circles, bees in second generation nests; open circles, bees in first generation nests (foundresses). a, head width = 2.36 mm.

Second generation nests contained from 1 to 10 females (Table 1). Once provisioning for the second generation was well in progress (14–25 June), most inhabitants were inseminated (83% of 18 bees), and about half (56% of 18 bees) had ovaries with at least one developed oocyte. The mean ovarian width of 0.843 mm (SD = 0.302, $n = 15$) was not significantly different from that for foundress females. In nest 8, two of six females had very well developed ovaries; in nest 9, one of the two females had very well developed ovaries; and in nest 10, three of nine recovered females had very well developed ovaries. Insemination status was not correlated with ovarian development; two of the three uninseminated bees had well-developed ovaries. Summer bee wear was similar to foundress bee wear after 14 June; 79% of 14 bees had nicked or tattered wing margins and 82% of 17 bees had well worn mandibles. The mean size of summer females ($\bar{x}$ wing length = 8.91 mm, SD = 0.262, $n = 19$, $\bar{x}$ head width = 3.14 mm, SD = 0.198, $n = 23$) was not significantly different from that of foundresses based on head width. Ovarian width was not significantly correlated with head width ($r = -0.11$) (Fig. 8).

Because bees were not marked and wear of summer females was similar to that of spring females, I could not determine if the foundress remained in each nest throughout the second generation. In the one nest excavated just after the beginning of the second generation (no. 7), the three bees captured were newly emerged adults, but the one bee that escaped must have been reproductive and was probably the foundress (there were only three vacated cells from the first generation, Fig. 6). All three recovered bees were uninseminated and had completely undeveloped ovaries. The mean size of these bees plus three others reared from first generation

pupae ($\bar{x}$ wing length = 8.83 mm, SD = 0.139, n = 5; $\bar{x}$ head width = 3.13 mm, SD = 0.057, n = 6) was slightly smaller than that of foundress females, the difference in head width being significant at the 5% level. The size difference between these first generation "workers" and the foundress "queens" was 1.2%, based on wing length, or 3.7%, based on head width.

A summary picture of the second generation, based on admittedly few data, is that the spring foundress remains in her nest at the beginning of the second generation, when the newly emerged daughter females act as uninseminated, non-reproductive workers. Within two weeks most of these females mate and develop ovaries to various degrees, so only about half of the summer bees are nonreproductive. Castes are then poorly defined, and reproductive status is not correlated with size. The "classic" worker, uninseminated with undeveloped ovaries, is then almost nonexistent (1 of 18 females). Nest no. 11, with one female, suggests that single summer females may also initiate or remain within nests.

In Utah, foundresses remain in their nests during the second generation and act as queens and guards, and are in flight for 2–3 weeks into the second generation. The first generation females all act as workers, unless the foundress queen dies, when one of her daughters becomes guard and principal egglayer. Nests contain 2–5 workers. Nye presented no data on size or ovarian status, but his summary indicates well-defined behavioral castes based on generation overlap.

Nest associates, predators, and guarding.—Two mite species were the most commonly recorded inquilines in *H. farinosus* nests in Davis. Scutacarid mites, *Imparipes americanus*, were collected from cells or adult bees in 8 of the 11 nests. Adult female mites clung to hairs of female bees, preferentially on the lateral surfaces of the propodeum bordering the posterior carinae, near the hind coxae. In the nests, occasional female mites were seen on provision masses and in cells containing developing bee larvae. Numerous mite larvae, males, and newly emerged adult females occurred on moldy feces in pupal cells of nest no. 10, and females also occurred on pupal and newly emerged adult bees. The life cycle of *I. americanus* appears identical to that of the closely related *I. apicola* (Eickwort, 1979) and both are presumably fungivores. *Imparipes americanus* was originally described from a specimen recovered from an adult *H. farinosus* in 1904 (see Delfinado and Baker, 1976) and has been studied by Cross and Bohart (1969) in association with the alkali bee, *Nomia melanderi*, where it is phoretic on 87% of adult female bees and does not harm bee brood.

The second mite was a species of *Histiostoma* (Histiostomatidae, previously Anoetidae), related to *H. halictonida*¹ (Woodring, 1973). It occurred on adult bees or in cells of 8 of the 11 nests, 6 of which also contained *I. americanus* (thus only one nest, no. 2, did not yield mites). Deutonymphs (=hypopi) attached by their ventral opisthosomal suckers to the wings and metasomal tergum 1 of adult female bees. Adult female mites were first seen in cells containing half- to two-thirds-developed bee larvae, and mite larvae and protonymphs occurred on the surfaces of prepupae and young pupae, while deutonymphs occurred on older pupae. The life cycle is similar to that of *H. halictonida* in nests of *Halictus rubicundus*

¹ *Histiostoma halictonida* and related species of *Histiostoma* associated with halictid bees, including the two species mentioned in this paper, belong to the genus *Anoetus* according to B. M. O'Connor (in prep., pers. comm.).

(Woodring, 1973; Eickwort, 1979), and like that species it presumably feeds on microorganisms and does not harm its host. Nye also recorded histiostomatid mites (as "*Histiogaster*," an acarid genus) in Utah nests of *H. farinosus*, as well as the heterostigmatid mite *Trochometridium tribulatum*, which I did not observe.

I recorded no other inquilines or parasites in cells of California *H. farinosus*. However, nest burrows were frequently usurped by the leafcutter bee *Megachile coquilletti* at both sites along Putah Creek in June. One nest (no. 9) excavated on 14 June still was actively used by *H. farinosus*, which reached its cells by a detour tunnel dug around the portion of the burrow usurped by *M. coquilletti*; both species used the same entrance. In the remainder of the seven usurped nests, adult *H. farinosus* were not present in the burrows although viable halictine brood were intact in cells below the *M. coquilletti* nests. A separate note is being prepared for publication on this bee.

In one of the usurped nests, ants (*Conomyrma*, *insana* species group) occurred in the burrow above the *M. coquilletti* nest but did not occur in the *H. farinosus* cells. Of more significance was the pavement ant, *Tetramorium caespitum*, which on 2 June eliminated one of the suburban lawn aggregations (site 3) of *H. farinosus*. Ants swarmed over the bee nest entrances, dragging dead adult female bees (Fig. 4). According to the homeowner who alerted me about this raid, the bees were alive when brought to the surface by the ants. Bee brood was not present on the surface. Schultz (1982) described raids of the pavement ant against nests of the alkali bee, *Nomia melanderi*. Nye recorded ants (?*Tapinoma* sp.) invading nest cells of Utah *H. farinosus*.

Nye also recorded *Sphecodes arvensiformis* (Halictidae), *Dasymutilla* sp. (Mutillidae), *Bombylius major* and *B. albicapillus* (Bombyliidae), *Leucophora obtusa* (Anthomyiidae), *Nemognatha lutea* (Meloidae), and *Rhipiphorus* sp. (Rhipiphoridae) as nest parasites. An unidentified aphelenchoidid nematode and *Acrostichus* sp. are phoretic in the reproductive tracts of Davis *H. farinosus* (Giblin et al., 1981). Nye recorded the fungus *Ascophæra ?apis* on feces in the cells in Utah. Feces were also mold-infested in the Davis cells, but only three cells contained dead, fungus-covered brood or provision masses. *Philanthus crabroniformis* (Sphecidae) (Alcock, 1974) and *Mallophorina guidliana* (Asilidae) (Nye, 1980) have been recorded as predators of foraging adult bees.

Nest guarding was observed in summer nests in Davis. When a guard bee was probed with a stem, it bent into a C-shape so both its open mandibles and the apex of its abdomen were directed towards the intruder. This position is unlike that observed in most halictines, where the head or the abdominal dorsum of the guard effectively blocks the entrance. The nest entrance of *H. farinosus* is relatively wide, allowing the simultaneous presentation of sting and mandibles. Nye also recorded nest guarding, but did not note the C-posture. He stated that the foundress queens were the principal guards in second generation nests.

Halictus ligatus

The three nests were in bare soil in the Putah Creek bank, near *H. farinosus* nest site 2. On 19 May, the entrances were open, unguarded, and narrowed (diameters 3.6–3.7 mm) but not conspicuously smoothed or rounded. Bees brought pollen into two nests. When excavated on 21 May, each contained one foundress female, which was inseminated with well developed ovaries. The two fully ex-

cavated nests were 19.5 and 20.5 cm deep, vertical, unbranched, with 14 and 8 cells respectively (Fig. 9). One nest had a 3 cm horizontal burrow just above the cells; this may represent the "forage cell" reported by Chandler (cited by Michener and Bennett, 1977). Top cells were 9.0 and 6.5 cm, and bottom cells 16.5 and 16.5 cm deep, respectively. Burrow diameter was about 6.5 mm. Cells were similar to those previously reported for *H. ligatus* (Michener and Bennett, 1977), 11.0–12.5 mm long ($\bar{x}$ = 11.60 mm, SD = 0.548, n = 5) by 5.5–6.5 mm wide ($\bar{x}$ = 6.02 mm, SD = 0.356, n = 5) and at a slight angle (6° – 12° , n = 3). Cell contents ranged from eggs to pupae. Four females were reared from pupae of one nest; their mean head width (2.96 mm, SD = 0.014) was smaller than that of the three foundresses from the nests (3.10 mm, SD = 0.110), giving a 4.4% size difference between the presumptive queen and worker castes.

One cell contained a very small muscoid dipteran larva in addition to a live, half-developed bee larva. Histiotomatid mites occurred in cells in one nest, the instars associated with the different developmental stages of the bee as described for the histiotomatid associated with *H. farinosus*. The mites associated with *H. ligatus* and *H. farinosus* belong to different, although closely related, species of *Histiostoma*. *Histiostoma* also occurs in *H. ligatus* nests in New York (Litte, 1977). Nematodes were abundant in the feces of pupal cells. Giblin et al. (1981) have recently described the relationship between the nematode *Acrostichus* sp. and Davis *H. ligatus*.

The Davis *H. ligatus* differ most strikingly from cool temperate populations in the number of cells in the foundress nests. As summarized by Michener and Bennett (1977), the average number of cells in single foundress nests in New York and Indiana ranges from 2 to 4, with maxima of 6 and 7. In contrast, the Davis nests contained 8 and 14 cells and were still being provisioned. The Davis nests resembled most warm temperate and tropical populations of *H. ligatus* (Michener and Bennett, 1977) in not being densely aggregated. Cool temperate foundress nests are often pleometrotic; my sample size was too small to preclude that possibility in Davis. The presumptive caste size difference of 4.4% is much smaller than similar differences in Indiana (14.5%) and New York (16.9%) populations (Michener and Bennett, 1977).

DISCUSSION

The subgenus *Halictus* is abundant and diverse in the Palearctic region (Michener, 1978), and at least 13 European and Asian species have been the subjects of nesting biology studies, as reviewed by Sakagami and Michener (1962), Michener (1974), Sakagami (1974, 1980), and Knerer (1980) (see also Batra, 1966b, and Ivanov, 1977): *Halictus* (*Halictus*) *cochlearitarsis*, *fulvipes*, *latisignatus*, *maculatus*, *paris*, *patellatus*, *quadricinctus*, *resurgens* (= *holtzi*, *turkommanus*), *rubicundus*, *sajoi*, *scabiosae*, *sexcinctus*, and *tsingtouensis*. These Palearctic species, plus the four North American species (*H. farinosus*, *ligatus*, *parallelus*, and *rubicundus*), present a common pattern of social structure (with exceptions as noted below): nests are founded in the spring by one or more inseminated females. Single foundress nests contain 4–6 cells. Males are typically represented by 5–10% of the first generation, although they are apparently absent in some populations of *H. sexcinctus*, *ligatus*, and *farinosus*. Summer nests contain 2–8 females that usually remain active through the summer until overwintering gynes become

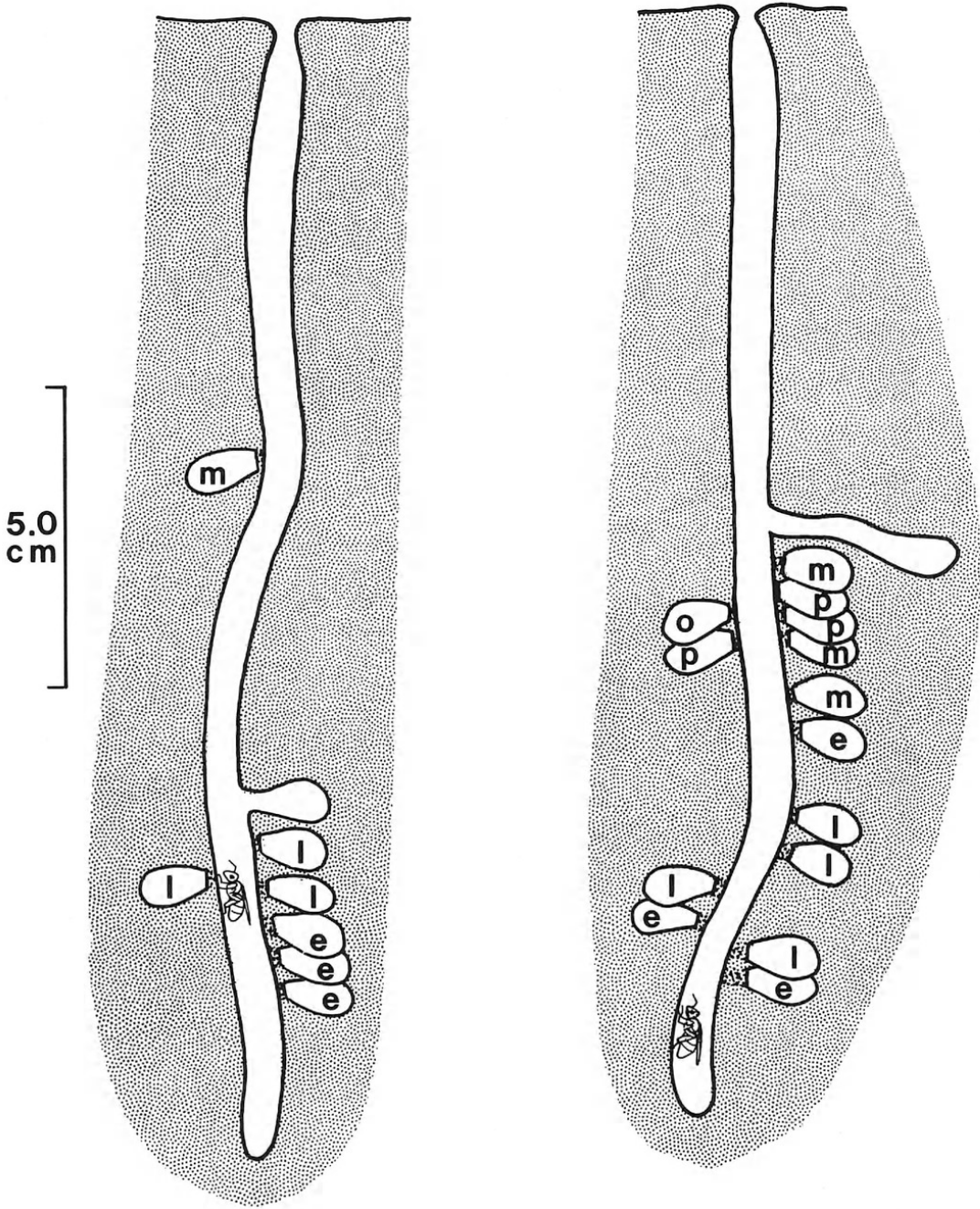


Figure 9. Foundress nests of *Halictus ligatus* excavated 21 May 1979 in Davis, California. Abbreviations as in Figures 5–7.

adults, unlike the short summer flight periods exhibited by eusocial *Evylaeus* (*H. sexcinctus* in Italy may resemble *Evylaeus* according to Bonelli, 1965). Foundress females remain in the summer nests as egglayers and they often guard. Except where males are absent in the first generation, from 4% to over 50% of the first generation females are inseminated, and foragers frequently have partially to well developed ovaries. Size differences between foundress “queens” and first generation “workers” range from 0 in one Swiss population of *H. scabiosae* (Batra, 1966a) to 5% in *H. maculatus*, 9% in German *H. scabiosae*, 12–17% in *H. ligatus*, and 17% in *H. latisignatus* (Sakagami, 1974). The latter Indian species has the

most distinctive castes of any analyzed *Halictus* (Batra, 1966b) and is the only member of its species group (Michener, 1978).

The California *H. farinosus* is unique among social *Halictus* in the large number of cells in typically monogynous spring nests; about twice that of any other species. This is not a species characteristic because Utah nests contain many fewer cells. It probably reflects the exceptionally favorable weather for foraging that is typical of California springs, in which foundresses can continuously provision cells. This hypothesis is supported by the large cell numbers in Davis *H. ligatus* foundress nests.

The poorly defined castes in summer nests of California *H. farinosus* are not unique among *Halictus*, although the lack of correlation between body size and ovarian development, the 83% insemination rate, and the 56% ovarian development rate make this population among the most weakly social of the temperate species. I hypothesize that second generation nests may start out as eusocial colonies, with the foundress queen dominating her worker daughters, but as the summer progresses the foundress dies or ceases to dominate and her daughters mate and their ovaries variously develop, resulting in a semisocial colony. This parallels the development in tropical *H. ligatus* nests (Michener and Bennett, 1977).

Halictus social structure is not fixed within a species and can be adapted to a particular climate by a population, as had been amply demonstrated for *H. ligatus* (Michener and Bennett, 1977) and in less detail for *H. scabiosae* (Batra, 1966a), and which Nye and I show for *H. farinosus*. The "classic" eusocial *Halictus* colony, with a foundress queen producing a second generation with the aid of her unmated, nonreproductive worker daughters, may be an adaptation to a temperate climate with a limited foraging season. Under these conditions selection favors distinct castes: the harsh spring favors a queen that budgets her time and energy and thus produces a few workers. The short summer prohibits these daughters from starting their own nests and favors a queen (and by kin selection also her worker daughters) that can reproductively dominate them and thus enforce efficient provisioning of gyne and male cells. The terms "primitive" and "advanced" may be meaningless in a phylogenetic sense when applied to caste differences within *Halictus*, as the different states may be simply expressions of the same genome under different climatic regimes.

However, eusocial behavior may well have characterized the ancestral *Halictus* species. All studied species of *Halictus* (*Seladonia*), the sister subgenus of *Halictus* s.s., are eusocial (Sakagami, 1980), as are all but a few *Halictus* s.s., Knerer (1980) cited *H. (H.) farinosus* and *parallelus* as being solitary, but he was mistaken about *farinosus*, and *parallelus* is social in Massachusetts, where Packard (1868) described a nest excavated on 16 July with 4 adult females and over 20 cells, containing young larvae to pupae. Knerer also recorded *H. sexcinctus* as being solitary in France, but Bonelli (1965) described eusocial colonies of that species in Italy. The best substantiated solitary European species is *H. quadricinctus*, although more than one female may occasionally occupy a nest (Grozđanić, 1969; Marikovskaya, 1972). Sakagami (1980) has recently demonstrated exclusively solitary nesting in *H. tsingtauensis* in Japan. He predicted that a social species might become solitary in colder parts of its range, where only one generation per

year can be completed. Multiple reversion to solitary existence from eusocial ancestry is a more parsimonious hypothesis than the reverse for *Halictus*.

As Michener (1974), Knerer (1980), and Sakagami (1980) point out, nearly all species of *Halictus* s.s. and all species of *H. (Seladonia)* share a common pattern of nest architecture: horizontal or slightly sloping cells connected to the burrow by laterals shorter (usually much shorter) than half a cell length, not clustered in a comb or surrounded by a cavity. Since the primitive halictine nest has long laterals leading to cells (Sakagami and Michener, 1962), the genus *Halictus* is characterized by an apomorphic nest architectural feature. However, two solitary, univoltine species, *Halictus quadricinctus* and *sexcinctus* sensu Knerer, deviate from this pattern.

Halictus quadricinctus nests have closely clustered cells surrounded by a cavity, much like those of eusocial *Evyllaes*. Despite its nests, *H. quadricinctus* is morphologically not a distinctive species, belonging to Michener's (1978) group 3, as does *H. farinosus*. The construction of a comb and cavity is not as unique as it might seem. Knerer (1980) notes three other species of halictines in which it appears facultatively, and a female of *H. rubicundus* tightly clustered its cells and surrounded them by burrows which formed an imperfect cavity when forced to nest in moist soil in my flight room. L. Packer (pers. comm.) has observed a similar phenomenon in laboratory-reared *H. ligatus*. Moreover, Marikovskaya (1972) provided diagrams and photographs of some nests of *H. quadricinctus* without cavities, as well as of nests more typical for this species. The construction of a comb of cells in a cavity thus appears to be an autapomorphic feature of *H. quadricinctus*, derived from typical *Halictus* nest-building behavior and not expressed under all conditions.

The population of *H. sexcinctus* studied by Knerer (1980) in France had cells connected to the burrows by long (11–18 mm) laterals. Knerer suggested that this is an adaptation for nesting in sand. While a nest with long laterals is otherwise considered to be primitive, I accept Knerer's hypothesis that it represents a reversal in *H. sexcinctus* from a typical *Halictus*-nest ancestry. The differences between Knerer's population and Bonelli's (1965) Italian population, with nests with short laterals and a bivoltine, eusocial seasonal cycle, suggest that two different species were involved.

The genus *Halictus* is large and diverse, yet quite clearly monophyletic (Michener, 1978). It is thus an excellent taxon for testing the value of nest architecture for classification. I conclude that nest structure is neither worthless nor a panacea. A common pattern does characterize the genus, but it has been readily modified into different types in response to edaphic conditions in ecological and evolutionary time.

SUMMARY

In the Central Valley of California, *Halictus (Halictus) farinosus* makes monogynous foundress nests that typically contain 11 or more cells, twice the number of any other *Halictus* species. Both males and females are produced in the first generation, and 83% of first generation females are inseminated. Castes are poorly distinguished after two weeks into the second generation; 56% of nest bees have developed ovaries, and there is no significant correlation between size and ovarian

development. In *Halictus (Halictus) ligatus*, monogynous foundress nests produce up to 14 or more cells and caste size differences appear less than half those reported for cool temperate populations. *Histiostoma* spp. (Acari: Histiostomatidae) are nest associates of both species of *Halictus*, *Imparipes americanus* (Acari: Scutacaridae) is a nest associate of *H. farinosus*, *Megachile coquilletti* (Hymenoptera: Megachilidae) usurps *H. farinosus* nest burrows, and *Tetramorium caespitum* (Hymenoptera: Formicidae) can destroy nest aggregations of *H. farinosus*.

Eusocial nesting is hypothesized to be primitive in the subgenus *Halictus*; *H. quadricinctus*, *sexcinctus*, and *tsingtouensis* are hypothesized to have reverted to solitary, univoltine nesting. In eusocial species, castes are typically continuous; *H. farinosus* represents an extreme in the subgenus in the lack of morphologically distinguishable castes. Its social structure appears to be an adaptation to the climate of central California. *Halictus (Halictus)* nests are characterized by sub-horizontal cells connected to the burrow by very short laterals; the two exceptions to this pattern (*H. quadricinctus* and *H. sexcinctus*) are hypothesized to have secondarily evolved from it.

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