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Journal of Hymenoptera Research 16:281-292 (2007) <http://biostor.org/reference/389>

Keywords: Halictidae; Halictus; Halictus hesperus; Halictus ligatus; Halictus pinguismentus; Halictus tripartitus; Hymenoptera; Quercus douglasii; Seladonia; Sphecidae



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Phenology and Social Organization of *Halictus (Seladonia) tripartitus* (Hymenoptera: Halictidae)

LAURENCE PACKER, ANNE-ISABELLE D. GRAVEL AND GRETCHEN LEBUHN

(LP, A-IDG) Department of Biology, York University, 4700 Keele St., Toronto,
Ontario M3J 1P3, CANADA

(GL) Department of Biology, San Francisco State University, San Francisco, CA, 94132, USA

Abstract.—We present data on the social biology of *Halictus (Seladonia) tripartitus* Cockerell based upon samples from California. This bee is at least partially eusocial and overwintered gynes and first brood workers differed in size by 5.14%. 35.5% of the first brood workers had developed ovaries, 11.2% had ovaries with the equivalent of at least one fully developed oocyte but less than 14% were mated. In July and August, female reproductive options seemed highly variable: approximately 55% were sterile workers, 2.6% had better developed ovaries than spring foundresses and over 20% had at least the equivalent of one fully developed oocyte whereas an additional 20–30% may have been capable of overwintering as gynes. Ovarially developed workers were larger than those that remained sterile. Sixteen to 28% of the late summer workers were mated, but mated individuals were not more likely to have developed ovaries or to be larger than unmated bees. We discuss these findings in the light of the climate of the study area and compare this species with other members of its subgenus.

Detailed assessment of the social organization of halictine bees requires painstaking field observations and nest excavations over the course of several flight seasons. Nonetheless, useful information can be obtained from less detailed analyses. Because of the evolutionary lability of sociality in these bees, even comparatively superficial data can be of utility in terms of plotting presence or absence of sociality upon a phylogeny or in obtaining estimates of sociobiologically important variables such as levels of morphological and physiological caste differentiation (e.g. Dunn et al. 1998).

The subgenus *Seladonia* (of the genus *Halictus*) contains species that are primarily solitary, such as *H. (S.) virgatellus* Cockerell (Eickwort et al. 1996), some with weak eusociality (Michener's 1974 terminology for social categories is used herein) as in *H. confusus* Smith (Dolphin 1971) to others with the largest colony sizes ever recorded for a halictine - *H. (S.) lutescens*

Friese (Sakagami and Okazawa 1985) or the largest morphological caste differentiation - *H. (S.) lanei* Moure (Janjic and Packer 2001). However, it should be cautioned that data for these, and most other species in the subgenus, are mostly fragmentary.

Halictus (Seladonia) tripartitus Cockerell is a halictine for which the only sociobiological data available are i) the surprising observation that, at a nest aggregation, smoke blown down one nest entrance came up out of the other entrances, demonstrating that the nests were connected underground (Eickwort personal communication 1988) and ii) a statement that the species is solitary (Amdam et al. 2006). It is a somewhat divergent member of the subgenus, forming the sister group to the remainder (Danforth et al. 1999), probably along with two rare species, *H. harmonius* Sandhouse and *H. pinguimentus* Janjic and Packer (Janjic and Packer 2001, Janjic and Packer unpublished data).

For a halictine population with an archetypal eusocial phenology (and indeed other annual eusocial insects in temperate climates), only mated and comparatively unworn females are expected to survive the winter. In spring they establish nests, their wings and mandibles increase in wear and their ovaries become well developed as they produce a brood composed primarily of worker females. Individuals in this brood are usually smaller than their mother and have reduced levels of ovarian development and a low frequency of mating (partly dependent upon the availability of males produced in the "worker" brood). Depending upon the length of the flight season, additional broods, primarily of workers, may be produced. Towards the end of the colony cycle, a brood composed of males and next year's colony foundresses is produced. Much of the variation in these parameters can, to some extent, be estimated from field collected samples in the absence of nest excavations (Dunn et al. 1998). In this paper we present some phenological and social organisation data for *H. tripartitus* based upon field samples, in order to add to the intensity of taxonomic sampling for such data in these behaviourally diverse bees.

MATERIALS AND METHODS

Sampling.—*Halictus tripartitus* adults were collected on the Kunde Wine Estate, 2.3 km southeast of Kenwood in Sonoma County, California, USA (38°24'15N, 122°31'43W). This site is a low-elevation, gently sloping oak woodland dominated by blue oak (*Quercus douglasii*), adjacent to a large vineyard. The oak woodland consists of 4–10 m tall trees that are generally widely spaced with few shrubs interspersed among them. At the site, a 100 m² sampling plot was established.

Bees were sampled in 2002 and 2003 on clear, low wind days. As preliminary data and previous monitoring studies show that different colored pan traps attract different

species of bee (Leong and Thorp 1999), the bee fauna was surveyed using a recently developed standard protocol which utilizes a mix of sweep-netting and pan trapping (protocols can be found at <<http://online.sfsu.edu/~beeplot>>). Pan traps were set out between 09:00 and 15:00 and sweep-netting was done for one hour in the morning and one hour in the afternoon per sampling day.

Some samples of females from 2003 were preserved in 70% alcohol and this permitted dissection for sociobiological data (see below). All samples collected in 2002 were pinned so only phenological data could be obtained from them.

Sociobiological Data.—The preserved bees were observed under a microscope to evaluate alar and mandibular wear (based upon the right hand side), measure head width, and dissect females for insemination and ovarian development status following slight modifications of standard protocols (Ordway 1965, Abrams and Eickwort 1980). Mandibular wear was scored on a scale from 0 – completely unworn, apex sharp; to 6 – mandible worn away to the base of the subapical tooth. Wing wear was assessed by counting the number of nicks in the wing margin, completely abraded wings were scored as having 15 nicks – the number that seems to result in complete abrasion of the margin. Total wear was calculated by adding the scores for wing and mandibular wear. It is useful to exclude freshly emerged adults from some analyses, such as of ovarian development and mating, because they may not have had enough time to mate or develop their ovaries. Consequently, in many analyses only bees with a total wear score greater than one were considered. Comparisons of ovarian development among samples were performed with bees parasitized by conopids removed from the sample. In later samples, when a mixture of ageing workers and newly emerged gynes might be expected, putative examples of the latter were assumed to have

a total wear of at most one and to have entirely undeveloped ovaries. Individuals with a total wear of three or more and with completely undeveloped ovaries were assumed to be permanently sterile workers in these samples. This protocol seemed appropriate in this study as these bees appear to become worn rather slowly, their wings seem to become "nicked" particularly slowly.

The spermatheca of each bee was observed for sperm, which make the otherwise glassy-transparent spermatheca opaque. On the few occasions when there was uncertainty as to whether a bee had mated or not, the spermatheca was gradually squashed between a cover slip and a microscope slide under high magnification to look for spermatozoa. Ovarian development was evaluated by estimating the proportion of a fully developed oocyte present in the bees and summing them across the 6 ovarioles. Bees with developed ovaries (defined as with at least one ovariole with at least one quarter of a fully developed oocyte) are sometimes referred to as OD+ in the account that follows, bees without ovarian development are referred to as OD-. Caste size dimorphism is estimated as $(q-w)/q$ where q is mean putative queen head width and w is mean putative worker head width.

Climatic data.—Because weather variation, both within and among years, influences sociobiological parameters for sweat bees (Richards and Packer 1995), we report temperature and rainfall data for the study area both in terms of data from the period when bees were sampled and for longer term average conditions. Data were taken from the Santa Rosa Airport Weather Station as indicated on the following web-pages: <http://www.pressdemocrat.com/nbwx/srweather/index.cfm> and <http://www.wunderground.com/history/airport/KSTS/1993/3/1/MonthlyHistory.html#calendar>. Data presented here are for mean daily temperature and rainfall for the months of March through August 2002 and

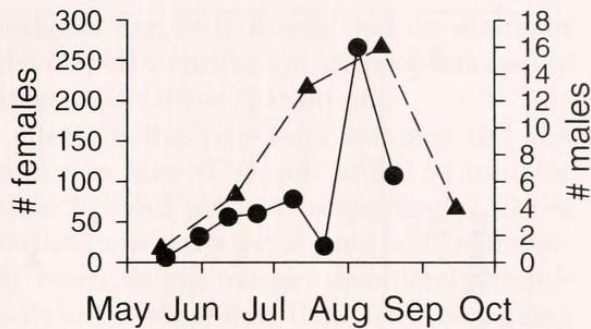


Fig. 1. Phenology of *H. tripartitus*. The left-hand axis indicates the number of females (●) while the right axis shows the number of males (▲), all collected in 2002.

2003, along with averages and maxima and minima for the same months over the 10 year period 1992–2001.

RESULTS

Phenological Patterns.—During the May–September period, 2002, a total of 765 *H. tripartitus* were collected at the Kunde Wine Estate. Of these, 726 were females and 39 were males. Numbers of *H. tripartitus* females increased gradually, nearly at a constant rate, from May to mid-July (Fig. 1) peaking at the beginning of August after a temporary decrease in sample size, and then decreased rapidly until the end of the season. Males show a similar pattern, but peak in the sampling period after the females. The discrepancy between the number of males and number of females in the samples is surprising; even at the peak of male abundance, there are approximately 8 times as many females as males. Based upon observations of museum holdings, this ratio would seem not to be an artefact as males of *H. tripartitus* are rare in collections (Packer unpublished observations).

The alcohol preserved material demonstrates that the species is active as early as March (see below), and inspection of museum holdings shows that a few females can be found as late as October (Packer unpublished observations).

The March 28th sample of dissected bees suggest that nest initiation had only just begun at this time: only 39% of the bees

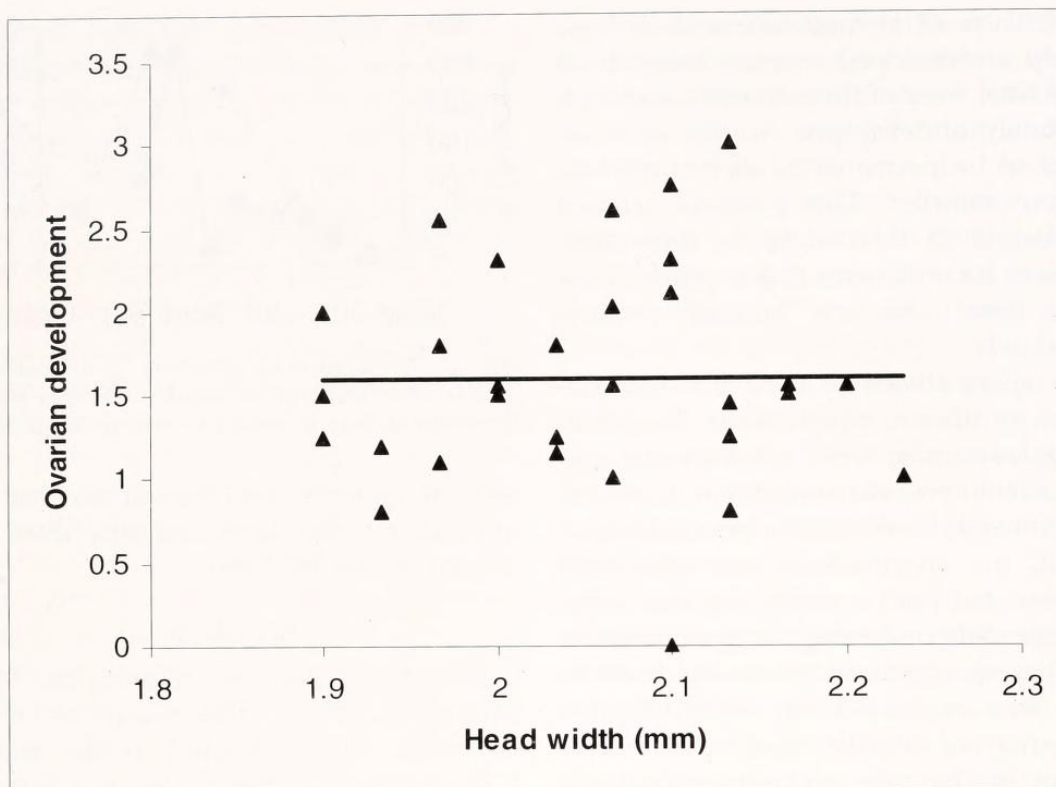


Fig. 2. Ovarian development and size variation in females of the May sample.

had mandibular wear, 16% had wing wear and 34% of them had some ovarian development with mean summed oocyte fractions of 0.16 per individual (Table 1). There was no size difference between ovarially developed and undeveloped females (mean head width OD+ females = 2.04 mm, SD = 0.11, n=54; OD- females head width = 2.06 mm, SD = .093, n= 28; $t = 0.93$, ns). Almost all females mated (97.2%), both unmated females were above average size for the sample.

In contrast, the May 16th sample was entirely of mated bees with worn mandibles, 94% had worn wings and all except a parasitized individual had developed ovaries with the summed fractions of developing oocytes averaging over 1.6 per bee. Ovarian development was independent of bee size (Fig. 2). The mean size of March and May sample bees was 2.04 (SD = 0.10) and 2.05 mm (SD = 0.09) respectively, not significantly different ($t = 0.35$, $p > 0.5$).

Table 1. Summary sociobiological data by sample date.

Sample date	N	% of ♀ with mandible wear	% of ♀ with wing wear	% of ♀ mated	% of ♀ with* developed ovaries	Mean ovarian score*	Mean ♀ Head width
March 28	82	39	16	97.2	34	0.16	2.04
May 16	31	100	94	100	100	1.6	2.05
June 20	67	81.5	26	13.8	43	0.4	1.93
June 30	50	96	62	6.5	26	0.14	1.94
July 18	166	68.7	70.5	13.7	55	0.44	2.01
August 20	118	56	36.2	34.2	34.5	0.28	2.01

*Parasitised females omitted from ovarian development data.

The two samples from June show an increased variance in wear but decreased ovarian development in comparison to the May sample. On June 20th, 81.5% of the bees had worn mandibles, 26% had worn wings, 43% had developed ovaries and 13.8% were mated. This was the only sample in which unworn bees were significantly less likely to have developed ovaries ($\chi^2 = 7.18$, $P < 0.01$; all other samples $p > 0.16$), suggesting that many of these individuals were young and had not had time to develop their ovaries. Nonetheless, worn bees with undeveloped ovaries made up 46.5% of this sample. On June 30th comparable data are: 96% with worn mandibles, 62% with worn wings, 26% with developed ovaries (31% if only worn bees are included) and 6.5% were mated. These data suggest increased average age/activity levels of the bees over the intervening ten days but a decrease in ovarian development. The average sum of fractions of oocytes shows the same decrease over time, the values were 0.40 for June 20th and 0.14 for June 30th. Of all June bees combined, only one individual (ie < 1%) had more enlarged ovaries than the average individual in the May sample.

Ovarially developed worn bees were significantly larger than worn OD- bees in the June 30th sample (mean head width OD+ bees = 1.98 mm, SD = 0.076, n = 11; OD- = 1.92 mm, SD = .089, n = 28; $t = 2.1$, $p < 0.05$), but not in the June 20th one (OD+ = 1.95 mm, SD = 0.94, n = 23, OD- = 1.93 mm, SD = .096, n = 19; $t = 0.91$, ns). The proportion of bees that were mated did not differ between the two June samples (Fisher's exact test, $p = 0.35$).

The data suggest that these early summer bees are offspring of the generation sampled in March and May and that they represent a worker brood. The pattern of ovarian development and age in these bees suggests that more workers initiate ovarian development soon after eclosion than manage to maintain developed ovaries a short while later. Furthermore, the data

indicate that individuals that do maintain developed ovaries, are disproportionately larger than those that do not.

Bees in the two June samples did not differ in size (1.93 mm and 1.94 mm for June 20th and June 30th respectively). Three individuals collected in June were extremely worn, (wing margin completely abraded), suggesting that they may be ageing overwintered females, perhaps from multiple foundress associations. All three were mated, one was parasitized with a conopid larva (Diptera, Conopidae), one had no ovarian development, the remaining individual had $\frac{3}{4}$ of a developed oocyte. Inclusion of these individuals in the comparison of ovarian development data between worn and unworn bees did not alter the statistical patterns noted above.

The July 18th sample had a lower proportion of bees with mandibular wear than in June (68.7%), a higher proportion with worn wings (70.5%) and a higher proportion with developed ovaries (55%, 54.4% when only worn bees are included). Similar to the June 20th sample, 13.7% of females were mated. The wear differential between mandibles and wings suggests that bees at this time are performing relatively more foraging or less digging than in the earlier samples. The average sum of fractions of oocytes was 0.44 and 6 individuals (3.8%) had more ovarian development than the average overwintered female in May. Worn OD+ bees were significantly larger than worn OD- bees (head width OD+ = 2.02 mm, SD = 0.07, n = 82; head width OD- = 1.98 mm, SD = 0.09, n = 44 respectively; $t = 2.56$, $p < 0.05$). Overall, July bees were intermediate in size between the smaller June and larger earlier samples, averaging 2.01 mm in head width; the sample of six individuals with very well developed ovaries had exactly the same average head width as the rest of the sample.

On August 20th the proportion of bees with worn mandibles decreased to 56% while 36.2% had worn wings. The pro-

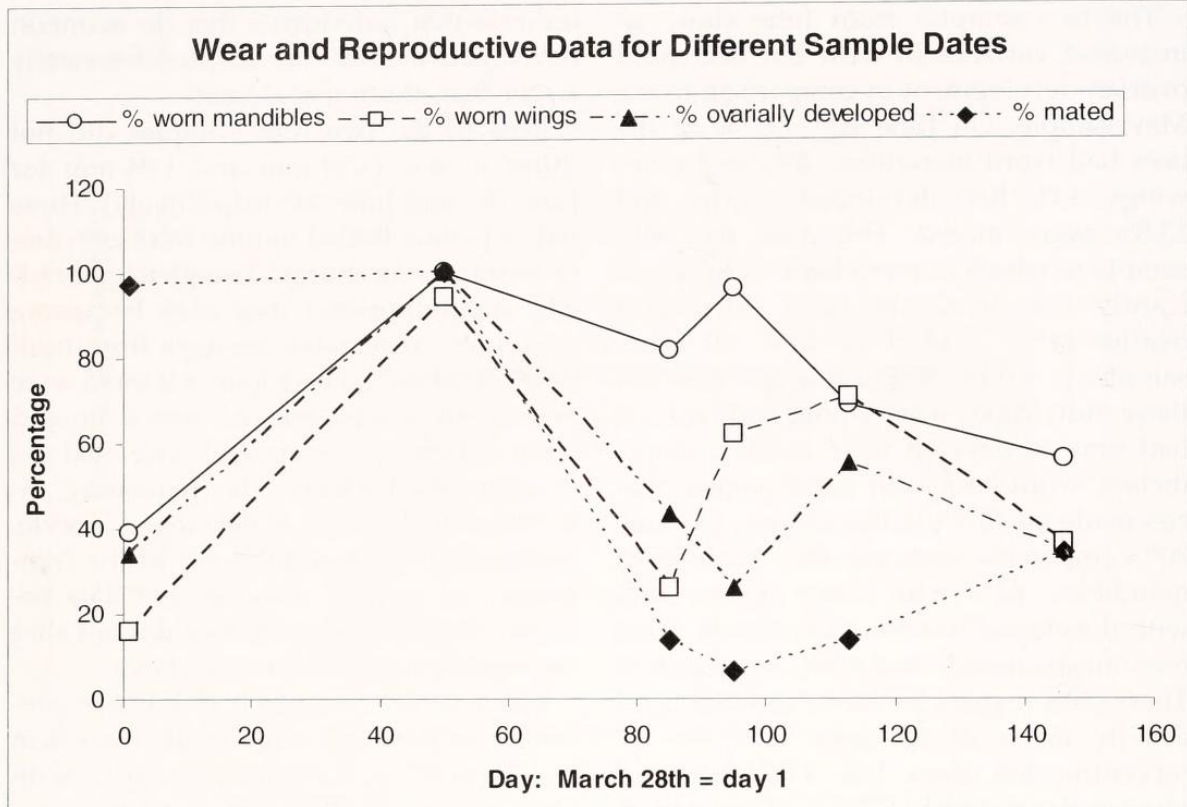


Fig. 3. Wear and reproductive variables for each of the samples of bees dissected.

portion with developed ovaries decreased to 34.5% (38.5% when only worn bees are included) and the percentage of females that had mated increased to 34.2%. The summed fraction of oocytes declined to an average of 0.28 and only one individual (<1% of the total) had ovaries that exceeded the average ovarian development of the May sample. As with the July sample, worn OD+ bees in August were significantly larger, on average, than OD- individuals (head width OD+ = 2.04 mm, SD = 0.10, n = 38; head width OD- = 1.99 mm, SD = 0.12, n = 28 respectively; $t = 2.73$, $p < 0.01$). Overall, the bees collected in August had an average head width of 2.01 mm, the individual with very well developed ovaries had a head width of 2.07 mm (not significantly larger than the sample as a whole, Mann Whitney U test, $p = 0.65$).

The wear and reproductive data discussed above are shown visually in Fig. 3.

Size variation among the four samples (March and May samples combined, two June samples combined) is significant (ANOVA, $F = 6.0$, $p = 0.0005$). Tukey's HSD test reveals that this result is due to the June bees being significantly smaller than the others ($p < 0.01$ for the overwintered female comparison and $p < 0.01$ and $p < 0.05$ for the comparisons with July and August samples respectively).

Caste.—The data above are consistent with the March sample consisting of overwintered females at the nest initiation phase, the May sample comprising the same generation individuals actively provisioning nests and with the June sample being first brood workers. The three heavily worn June bees perhaps represent subordinates in multiple foundress associations. Although this would require nest excavation data for confirmation, it is uncommon for solitary foundresses to forage for such an extensive period of time

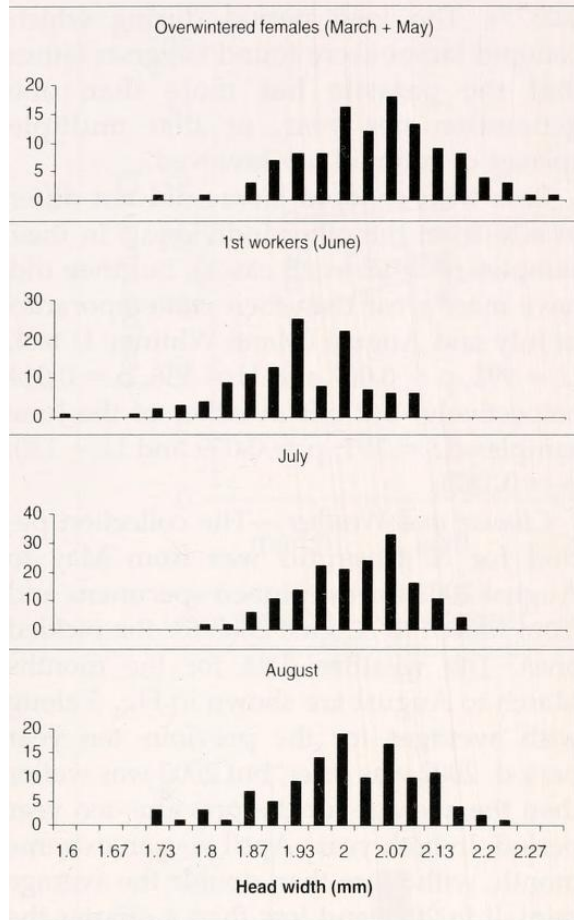


Fig. 4. Size variation (head width) among females from each of the months sampled.

or to become so heavily worn. If this is the case, then the putative gynes average 2.04 mm in head width (SD = 0.10) and the first worker brood 1.94 mm (SD = 0.09), the castes differ significantly in size ($t = 11.22, p \ll 0.001$) and the morphological size difference between gynes and the first worker brood is 5.14%.

Size variation data for the overwintered females, first brood workers and July and August females are shown in Fig. 4.

July and August females are not so easily categorised as to caste as they are expected to include some newly emerged gynes as well as ageing workers and perhaps some young workers also. We take ageing bees with undeveloped ovaries to be sterile workers, ageing bees with well developed ovaries (with total ovarian development at least equivalent to one fully developed oocyte) to be potentially reproductive workers and unworn bees with completely undeveloped oocytes to potentially be gynes.

Data for these three groups are shown in Table 2 separately for July and August. Interestingly, the sizes of the potential gynes in July are very similar to those for the overwintered females the previous March and May. The reproductive workers are also somewhat large, but their wear indices suggest that they do not represent the same overwintered females as were sampled in March and May as their index of wear is too low for them to have been active for the entire intervening period (only three of 40 have a higher index of wear than the average female in the May sample) and none of them are mated. The sterile workers are the smallest individuals in the sample.

The pattern for the same three classes of bee for the August sample is quite different. In August the sterile worker and potential gyne samples are identical in size but the reproductive workers are larger. Indeed, the mean size of the reproductive workers in August is the largest of any of the categories analysed in any time period. Even these, however, would not seem to be remaining overwintered females as only 4

Table 2. Sociobiological data for different "castes" of summer female. For explanation of caste designation see text.

Putative Caste	July		August	
	Head width (SD) N	% mated	Head width (SD) N	% mated
Sterile workers	1.99 (0.07) 22	13.6	1.99 (0.09) 10	60.0
Reproducing workers	2.02 (0.09) 5	0.0	2.10 (0.14) 5	0.0
Gynes	1.99 (0.09) 30	28.9	2.03 (0.08) 45	17.4

of the 15 have a total wear greater than the May sample and none of them are mated.

It would seem that the fates of bees eclosing in summer are highly variable. Some seem to remain strictly as workers, attaining high wear indices without developing their ovaries. A total of 55% of the July and August bees had a total wear index of 3 or more but had completely undeveloped ovaries. Such bees were smaller than the worn bees that had developed ovaries and the size difference between these apparent permanent workers and their contemporaries that have highly developed ovaries, with ovarian development greater than or equal to one is even larger: 3.8% ($t = 5.24$, $p \ll 0.001$) and 4.8% ($t = 4.54$, $p \ll 0.001$) for July and August samples respectively.

For none of the samples of worn bees was there a significant association between ovarian development and mating ($p > 0.5$ in all comparisons). Similarly, the mated bees were not larger than unmated ones (worn bees only) in any of the analyses ($p > 0.5$ in each case) except for the July sample in which the mated bees were significantly larger than the unmated ones (head width mated = 2.05 mm, SD = 0.08, $n = 14$, head width unmated = 1.99 mm, SD = 0.06, $n = 75$; $t = 7.14$, $p \ll 0.001$).

Parasitism.—One female was found with a large nematode in the metasoma, she was from the March sample of overwintered females. Twenty females were parasitized with one conopid larva in each metasoma and three contained two parasite larvae. It is likely that these parasitism rates are underestimates as small conopid larvae and nematodes would likely have been missed in the dissections, especially if they were primarily underneath the first metasomal tergum, which was not removed.

Of the 23 females with conopids, one was found in the May sample, four each in the two June samples, eight in July and six in August. The overwintered females were significantly less affected by conopids than were later females (Fisher's exact test $p =$

0.0377). The long period during which conopid larvae were found suggests either that the parasite has more than one generation per year, or that multiple species of conopid are involved.

Bees with conopid larvae did not differ in size from the other individuals in their samples ($p > 0.2$ in all cases), but they did have more wear than their contemporaries in July and August (Mann Whitney U test, $U = 991$, $p = 0.007$ and $U = 536$, $p = 0.014$ respectively) but not in either of the June samples ($U = 191$, $p = 0.059$ and $U = 130$, $p = 0.187$).

Climate and Weather.—The collection period for *H. tripartitus* was from May to August 2002 for the pinned specimens and from March to August 2003 for the pickled ones. The weather data for the months March to August are shown in Fig. 5 along with averages for the previous ten year period. 2002 was drier, but 2003 was wetter than the average for the previous ten year period. In both years April was an extreme month, with more than double the average rainfall in 2003 and less than a quarter the normal amount in 2002. The temperature data show that 2002 varied little from the average conditions whereas in 2003 April was cooler than any year between 1992 and 2002 and July was warmer than in any of these other years.

DISCUSSION

Halictine bees are well known for their variable social behaviour, not only within and between populations and species but also among individuals within a colony. Taken in their entirety, our data strongly support the view that *H. tripartitus* is primarily eusocial at our study site. Perhaps the strongest evidence for this comes from all overwintered females being mated whereas the first brood offspring were almost entirely unmated. Indeed, as a whole, the data are mostly consistent with the view that this species is a typical annual eusocial species with overwintered females initiating nests in March and

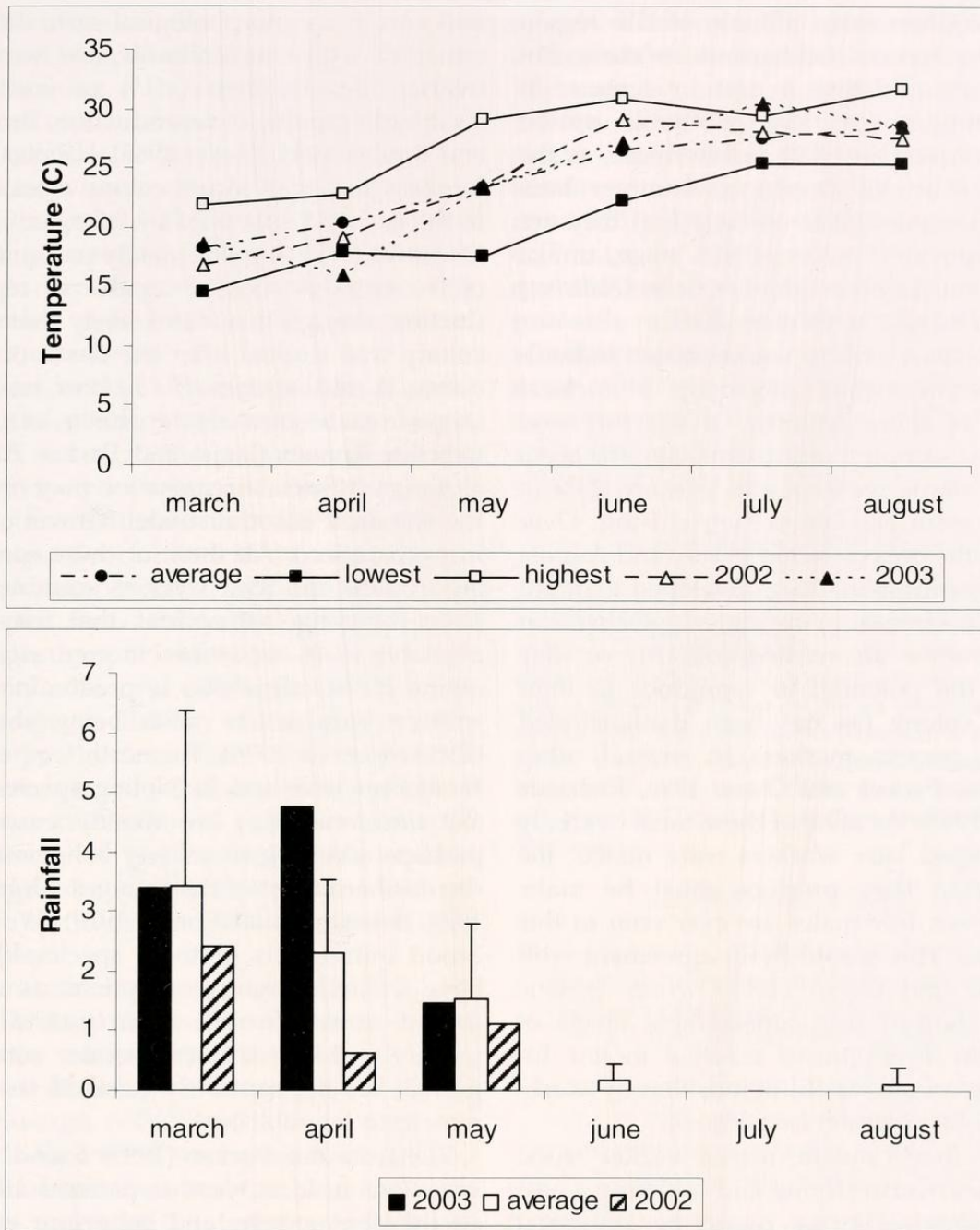


Fig. 5. Weather data for 2002, 2003 and summaries for the ten previous years 1992–2001.

foraging until May, workers emerging in June and overwintering gynes commencing emergence in July. Less usual features are the apparent multiple nest entrances, low frequency of males and the nature of the sample in August. We return to these three aspects towards the end of the discussion after considering worker fitness options and making comparisons between

H. tripartitus and other species of the subgenus *Seladonia*.

Fitness options for bees eclosing in summer within a eusocial family structure include remaining as a sterile worker, attempting to produce some offspring directly or initiating a nest either the same year as they eclose (Richards et al. 2003) or after overwintering (Yanega 1988). Given

the Mediterranean climate of the region and the dryness and hardness of the soil in summer, initiating a nest in summer is probably not a very profitable option (McCorquodale 1989). Furthermore, as the most ovarially developed summer bees were unmated, it is unlikely that they are founding new nests at this stage, unlike some summer females of *Halictus* (*Halictus*) *sexcinctus* (Richards et al. 2003).

Halictus tripartitus worker brood individuals seem to take advantage of at least three of these options. Of the July and August samples, approximately 55% seem to be sterile workers and perhaps 20% of them seem capable of reproducing. Over 2% of the bees collected in July and August had ovaries more fully developed than did the foundresses in spring, suggesting that either some are nesting solitarily or they have the potential to reproduce in their natal colony (as has been demonstrated using genetic markers in several other species, Packer and Owen 1994, Richards et al. 1995). As none of these most ovarially developed later workers were mated, the offspring they produce must be male. However, few males are ever seen in this species. This would be in agreement with Packer and Owen (1994) where genetic data showed that considerable levels of ovarian development resulted in few instances of successful oviposition by workers of *Lasioglossum laevisimum*.

The fourth option, mated worker brood females overwintering and initiating a nest the following spring, cannot be confirmed or refuted with the data at hand. It remains possible that brood divalency may occur in *H. tripartitus*. The easiest way to document this would be to mark large numbers of emerging "worker" brood females as they leave the nest and search for them when the foundresses begin activity the following spring.

Few species of the subgenus *Seladonia* have received detailed sociobiological investigation. The best studied is *H. (S.) hesperus* Smith, which has large colonies

and very large morphological caste differentiation with concomitantly low worker ovarian development (<1% of workers seemingly capable of reproduction, Brooks and Roubik 1983, Packer 1985). *Halictus (S.) lutescens* has even larger colony sizes and in the one nest excavated by Sakagami and Okazawa (1985) approximately one quarter of the workers seemed capable of reproduction, though it remains likely that this colony was studied after the death of the queen. A third species, *H. (S.) lanei*, has the largest caste size dimorphism of any halictine known (Janjic and Packer 2001), although its social organisation may not fit the standard eusocial model (Gravel et al. in preparation). All three of these species are tropical and their workers seem not to have the range of options that may be available to *H. tripartitus*. In contrast, the alpine *H. (S.) virgatellus* is predominantly solitary with a few nests being shared (Eickwort et al. 1996). The north temperate *H. (S.) confusus* and its sibling species *H. (S.) tumulorum* (L.) are weakly eusocial, perhaps reverting to solitary behaviour at the northern edge of their ranges (Dolphin 1971, Sakagami and Ebmer 1979). Worker brood individuals in these species likely have a similar range of options as suggested above for *H. tripartitus*, albeit usually within a shorter summer activity period, but appropriately detailed studies remain to be published.

Richards and Packer (1995) found that variations in local weather patterns affected the demography and behaviour of *H. (H.) ligatus* colonies: warmer and drier weather resulted in larger broods with better survival rates and lower nest-failure and more reproduction by workers. Thus, warm, dry weather resulted in weaker eusociality. Conversely, colder, wetter conditions gave rise to smaller workers with greater reproductive differentiation between the castes but also lower brood-survival rates and more nest-failure. Colder and wetter weather resulted in stronger eusociality. The area where *H.*

tripartitus was studied was unusually cold and wet in April of 2003, during foundress provisioning. If the weather influences this species in the same manner as it does with *H. ligatus*, it is likely that early summer colonies were smaller, with stronger physiological caste differentiation than is usual for this population. The poor weather in April may also explain the apparently extended period of activity of overwintered foundresses.

There are no detailed studies of social sweat bees from Mediterranean climates in North America. The restriction of precipitation to the winter and early spring is a feature that can limit the duration of colonies of social bees in the area and few individuals of *H. tripartitus* have been collected from late August onwards: even though temperatures are adequate for activity, the dry conditions severely restricts the availability of forage. It is likely that the late summer activity of this species is a comparatively recent phenomenon as at this time of year they rely upon flowering of plants that are maintained by agricultural irrigation. This could explain the unusual nature of the August sample.

Two other unusual aspects of this species' biology are worthy of comment, and may be related. First, the very low proportion of males, either as sampled here or in museum collections, is surprising. Towards the end of the colony cycle in most eusocial halictines, males are approximately as common as females, yet in *H. tripartitus* they are almost an order of magnitude less common. Second, the observation of nests apparently being connected underground is entirely unique among bees. It remains possible that males primarily search for mates underground, thereby uniting these two unusual phenomena. Certainly this species is worthy of more detailed field investigations, something we hope this paper will stimulate.

Lastly, the observation that worker ovarian development seemed to decline over

time is of interest. This phenomenon has been observed in numerous social insects. There are two main reasons this might be the case. First, the act of work might make it less likely that a bee has the energy resources to develop oocytes – which are remarkably large in comparison to bee body size in halictines. Alternatively, it could be that workers develop their ovaries primarily to coincide with male production when reproductive broods are protandrous. The fact that first brood workers are active at a time of year when few males are being produced in *H. tripartitus*, argues against the second explanation.

ACKNOWLEDGEMENTS

The senior author's research is funded by the Natural Sciences and Engineering Research Council of Canada. We are grateful for the comments of Miriam Richards on an earlier version of this manuscript and to Luana Sciuillo for processing the weather data. The junior author's research is funded by the Integrated Hardwoods Range Management Program. We also thank Cynthia Fenter, Erin Rentz and many SFSU students for their work collecting these insects.

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