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Lasioglossum (Dialictus) tenax (Sandhouse) (Hymenoptera: Halictidae) as a solitary sweat bee

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Summary

Nine nests of *Lasioglossum (Dialictus) tenax* were excavated near Calgary, Alberta, Canada over a time period encompassing the entire brood production period in 1988. Each nest contained a maximum of one active adult female, nest productivity peaked in mid July, protandry was noted and no significant size difference between foundresses and the earlier emerging females was detected. These data suggest that this species is solitary. These results are compared with data for the sympatrically nesting eusocial species *L. (D.) laevissimum.*

Introduction

The importance of bees of the subfamily Halictinae for studies of the origins of social behaviour in insects is widely acknowledged. Yet despite the large number of species that have received field study (Michener, 1990), the factors that have promoted eusociality remain poorly understood. One main reason for this is a dearth of phylogenetic information on behaviourally studied taxa such that it is not possible to place the observed social variation within a rigorous evolutionary framework (Packer, 1991). The little information available on this topic suggests that reversals from social to solitary behaviour are more easy to document than are recent origins of eusociality (Packer, 1990, 1991; Richards, in press). However, the data are rather biased as comparatively few solitary species have been studied, thus favouring sociality as an ancestral character state in any phylogeny. This places a premium on establishing which species are solitary. But it is often more difficult to prove that a species or population is solitary than to document an example of eusociality (Sakagami, 1980). However, the exclusion of eusociality as the predominant colony type can be made with some confidence from comparatively small samples if the data are entirely inconsistent with expected patterns under a eusocial colony cycle.

Among the genera and subgenera of Halictinae, bees of the subgenus *Dialictus* seem the most promising candidates for the study of the origins of eusocial behaviour because there are several species groups which are solitary and several which are primarily eusocial (Eickwort, personal communication). In this paper, I provide data on an apparently solitary species of the subgenus *Dialictus* – *Lasioglossum (Dialictus) tenax* (Sandhouse). Because comparatively small numbers of nests were excavated, the data are presented in full so that the bases for the conclusions regarding the apparently solitary nature of *L. tenax* can be evaluated.

Methods

Data on *Lasioglossum tenax* were obtained in the course of detailed studies of *L. (Dialictus) laevissium* carried out on the grounds of the University of Calgary Farm, Calgary, Alberta in the summer of 1988. For a full description of the study site see Packer (1992). Several additional halictine species also nested there but *L. (D.) laevissimum* was by far the most numerous. *Lasioglossum tenax* was readily distinguishable from the other species due to its small size, the presence of a weak acarinarium, and details of the surface sculpture, especially of the thoracic pleura and first abdominal tergum.

Most nests were discovered by brushing away the surface soil to reveal nest entrances. Standard nest excavation techniques were employed throughout (Packer and Knerer, 1986; Packer, 1992). Nests were excavated from early in the provisioning phase in June until August, after the commencement of brood eclosion. All excavations were performed before 900 hrs or after 1800 hrs when all foraging females would be inside the nest. Bee head width was measured to the nearest 1/20th of a millimetre. Female mandibular wear was scored and ovarian and mating status determined according to standard procedures (Packer and Knerer, 1986).

Table 1. Summary of nest contents for nine nests of *Lasioglossum (Dialictus) tenax*

		brood cell contents									
Date	Nest #	empty	pollen	larvae	pre-pupae	pupae		callows			foundress mandibular wear
						male	female	male	female	total	
27.6	1	0	1	0	0	1	0	0	0	2	2
27.6	2	0	2	0	0	2	0	0	0	4	3
29.6	3	0	0	1	0	0	0	0	0	1	3
15.7	4	0	3	2	1	1	1	1	1	10	4
15.7	5	0	1	2	1	1	0	0	0	6*	5
26.7	6	0	0	0	0	0	2	0	0	2	4
31.7	7	2	0	0	0	0	0	1	2	5	–
04.8	8	0	0	0	1**	2	2	0	0	5	5
04.8	9	0	1	0	2	0	0	0	0	3	6

* including one dipteran puparium
** diseased

Table 2. Size frequency data for male and female brood and foundress females of *Lasioglossum (Dialictus) tenax*

Head width (mm)	1.35	1.4	1.45	1.5
Foundresses	1	2	2	3
Male brood	2	2	1	2
Female brood	1	1	2	1

Results

Nine nests of *L. tenax* were excavated along the northern edge of a shallow bank surrounding a largely dried up pond. All had the standard *Dialictus* nest architecture with sessile brood cells arising from a vertical or almost vertical burrow. This structure was referred to as subtype IIIb by Sakagami and Michener (1962). Nest entrances were flush with the largely horizontal surface soil and were not hidden by vegetation. Two nest entrance diameters were measured at 1.7 and 1.8 mm respectively. Nest burrows varied in diameter from 2.0 to 2.8 mm with an average of 2.3 mm ($n = 5$). The depth of the shallowest cell was recorded as 6.5 cm in each of two nests and the greatest depth attained by the main burrow was 9.5 and 11.0 cm in these nests.

Provisioning began in spring (commencing in late May in this northern locality) but was interrupted by cool weather as indicated by two nests excavated at the end of June which contained a total of three male pupae and three pollen balls but no larvae or prepupae (Tab. 1). Provisioning continued until mid July at which time the first adult offspring eclosed. A maximum of 10 brood was produced in any nest.

Two out of 37 cells showed evidence of brood mortality, one contained the puparium of a dipteran and another contained a dead, deep red fully grown larva suggestive of infection by the bacterium *Serratia marcescens* (see Batra, 1965).

Each of eight nests contained one adult female with worn mandibles; seven of these females also had developed ovarioles containing yellow bodies (Billen, 1985) and sperm in the spermatheca (the abdomen of the remaining female was lost during excavation). Two of these nests also contained one or two young callow females with unworn mandibles and soft wings. An additional nest appeared to have been orphaned. Foundress mandibular wear increased during the summer with all females excavated after the end of June with abrasion extending to, or almost to, the inner mandibular tooth.

Protandry is suggested by the nest content data in that six male and two female pupae (including callow adults) were excavated before the middle of July and three male and six female brood were found after July 15th. This is significantly different from a null hypothesis of females being produced earliest as would be the case in a eusocial species (Fisher's exact test = 0.04). The sex ratio of the entire sample was as close to 1:1 as can be obtained with an odd sample size of 17.

There was no difference in the sizes of maternal and offspring female head widths (Mann-Whitney U test, $U = 22.5$, $p > 0.25$, $n = 8$ and $n = 5$ respectively) based upon population averages. Within two nests, the earliest female offspring was larger than the foundress, but two female offspring excavated later in the year were either the same size or smaller than their mother. Male brood did not differ significantly in head width from female brood (Mann-Whitney U test, $U = 19$, $p > 0.25$, $n = 7$ and $n = 5$ respectively). Size frequency data for male and female brood and nest foundresses are provided in Table 2.

Discussion

The evidence suggesting that L. tenax *is a solitary bee is as follows.*

i) Even though only nine nests were excavated these were sampled throughout the summer, giving ample opportunity for the discovery of eusocial nests if this were the predominant form of colony type in this species at this locality. Furthermore, excavation of four nests in July coincided with the active period of workers of the sympatric eusocial species *L. (D.) laevissimum* and yet each nest contained at most one active adult female.

ii) Eusocial species are expected to produce a female-biased brood during the early provisioning period (but see Packer, 1990) and then switch to a male-biased brood, normally after the emergence of the first workers. In *L. tenax* the entire offspring generation is seemingly protandrous.

iii) Most social halictines have morphological caste differences reflected in a smaller average size for workers and in almost all cases mothers are larger than the workers produced in their own nests (Packer and Knerer, 1986; Packer, 1992). Although the sample size here is small, the size variation between mothers and daughters in *L. tenax* is not consistent with its being a eusocial species.

iv) The number of brood cells produced by a north temperate eusocial sweat bee typically exhibits two periods of rapid increase representing worker brood and reproductive brood production. In *L. tenax*, maximum brood sizes were attained by the middle of July, whereas in *L. laevissimum* the average number of brood cells per nest increased dramatically in mid July coinciding with reproductive production. Furthermore, over 80% of *L. laevissimum* brood cells excavated in mid July contained pollen balls (Packer, 1992), whereas the corresponding figure for *L. tenax* was 25% (4 out of 16), suggesting the decline in provisioning towards the end of the active phase of a solitary species.

With none of the nine nests showing any of the characteristics of eusocial colonies, it is unlikely that this species is predominantly eusocial (indeed, a G test indicates that these data are significantly different from a scenario in which one third of the nests are eusocial, $G = 4.1$, $p < 0.05$). It seems safe to conclude that *L. tenax* is not a eusocial species at this study site and the absence of any multi-female nests in the sample of three excavated in June suggests that semisocial or communal behaviour is unlikely to be the preponderant colony type. It is concluded that *L. tenax* is a solitary species at this locality.

With an average productivity of 4.5 brood cells per nest from the middle of July onwards, this solitary species produced a slightly larger brood than did foundresses of the eusocial *L. laevissimum* during the spring provisioning phase in solitarily founded nests (Packer, 1992). However, reproductive brood productivity in the eusocial species exceeded the entire brood productivity of *L. tenax* by a factor of 5; although without data on nest failure rates for both species further sociobiological interpretation of these figures is not meaningful.

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