

THE NESTING BIOLOGY AND SOCIAL ORGANISATION
OF *LASIOGLOSSUM (EVYLAEUS) LATICEPS*
(HYMENOPTERA, HALICTIDAE) IN ENGLAND

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SUMMARY

An aggregation of *Lasioglossum (Evylaeus) laticeps* (Schenck) was discovered on the cliffs at Charmouth, Dorset, where nests were initiated in cracks in the clay soil. The cell clusters of both spring and summer broods were surrounded by a cavity which was enlarged as the number of cells increased. *L. (E.) laticeps* appears to have the most primitive social organisation of the four species of the *L. (E.) malachurum* species group for which data are available. Thus there is a high proportion of males in the first brood (24 %) and the morphological caste differences are slight: workers are, on average, 7 % smaller than the queens.

RESUME

**Le comportement de nidification et l'organisation sociale
de *Lasioglossum (Evylaeus) laticeps* (Hymenoptera, Halictidae) en Angleterre.**

Une bourgade de *Lasioglossum (E.) laticeps* fut découverte sur les falaises de Charmouth, Dorset, où des nids débouchaient dans des fissures de la glaise. Les rayons de couvain de printemps et d'été étaient entourés par une cavité, agrandie à mesure de l'augmentation du nombre de cellules. *L. (E.) laticeps* est une abeille sociale primitive, comme le démontre la proportion élevée des mâles dans le premier couvain (24 %) et les faibles différences morphologiques dans la caste femelle: les ouvrières sont, en moyenne, 8 % plus petites que les reines. Cette espèce semble avoir une organisation plus primitive parmi les quatre espèces du groupe de *L. (E.) malachurum* sur lesquelles on a des informations.

INTRODUCTION

Lasioglossum (E.) laticeps is a small, shiny, black bee very closely related to three of the most socially advanced halictine species: *L. (E.) malachurum*, *L. (E.) lineare* and *L. (E.) pauxillum* (EBMER, 1971). Although mainly a Central European and Mediterranean species, it occurs very locally on the South coast of Dorset, England where it has been observed nesting in joints in an old stone wall (NEVINSON, 1904). It has also been found nesting between the stones of a cobbled street in Linz and Vienna, Austria (EBMER, personal communication). In addition to its more unusual choice of nest sites, this species is of interest because a knowledge of its social organisation could help to elucidate the evolution of sociality in this group.

The nest site

A small aggregation of *L. laticeps* nests was discovered on the cliffs between Charmouth and Lyme Regis. This area of the Dorset coast is very unstable, being composed of incompetent clay soil overlain by sand and gravel. Slumping of the cliffs continually generates bare clay exposures and the terracing effect results in the formation of damp reed bed habitats as well as South facing slopes very attractive to sun loving Hymenoptera. The aggregation was situated on a 30° slope and occupied an area of about 15 square metres. The soil surface bore sparse vegetation, was very friable and much dissected by desiccation cracks. Beneath the dry surface the soil retained moisture very well, but embedded in the damp matrix were blocks of harder, drier clay up to 6 cm in thickness. The bees made their nests in the soft, damp clay and the harder soil.

Nest architecture

Nest entrances were situated in cracks in the soil surface and were often obscured by loose soil particles which had fallen into them. It was not uncommon to see returning, pollen laden foragers digging at this loose soil for several minutes before entering their burrows.

Tumuli were not observed around nest entrances, but excavated soil was packed into the cracks in which the burrows had been begun. Soil nesting halictines compact the lining of their burrows by tamping the soil with the tips of their abdomens. In the nests of *L. laticeps* it appeared that this was not done for the first one or two centimetres, probably because of the dry, friable nature of the soil and the unstable nature of the cracks.

Brood cells were built together in a cluster surrounded by a cavity in both the spring and summer broods. The clusters were supported by several broad, earthen pillars. That even the smallest brood clusters were surrounded by a cavity indicates that the cells were not simply carved out of the clay but built up, one by one, as the cavity was enlarged during the nesting phase

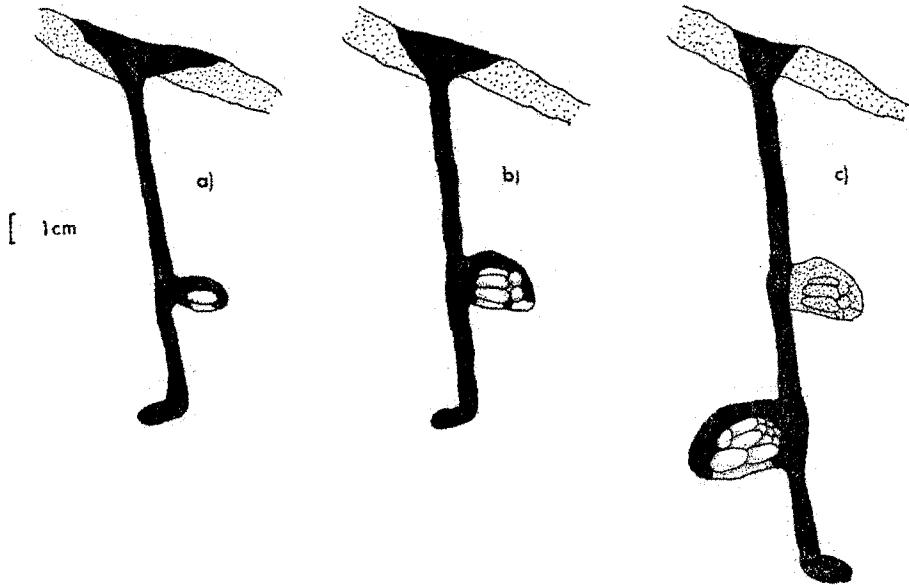


Fig. 1. — Nest construction in *L. (E.) laticeps*. The stippled areas at the top of each drawing represents soil packed into the crack in which the burrows are begun. a) Nest early in the first provisioning phase with one cell surrounded by a cavity. b) Nest at end of the first phase with a complete brood cluster and a cavity. c) Nest at the end of the second provisioning phase, the first brood cavity has been filled with soil from the excavation of the cells and cavity for the second brood.

Fig. 1. — Construction des nids de *L. (E.) laticeps*. Les déblais sont indiqués en pointillés et se situent dans la fissure à l'entrée des conduits. a) Nid neuf dans la première phase d'approvisionnement avec une cellule entourée d'une cavité. b) Nid à la fin de la première phase avec un rayon complet et une cavité. c) Nid à la fin de la dernière phase d'approvisionnement. La première cavité avait été remplie avec les déblais de construction des cellules du deuxième couvain et de la cavité secondaire.

(fig. 1). Although not all nest depths were recorded, cell clusters of the first brood were commonly between 6 and 10 cm below the surface whereas those of the second were a little deeper, ranging from 8 to 15 cm deep. A few nests were found in which the spring and summer clusters were at the same depth.

Unlike most cluster building *Lasioglossum*, the cells were not always aligned in the same direction: varying in their compass direction by as much as 90° from each other and varying in slope from 5° to 45° from the horizontal. Their walls were thicker than those of species such as *L. malachurum* and *L. lineare* and appeared more amorphous as a result. The cells also seemed to be more cylindrical in shape than in these species. These

three features may be due to a primitive nest architecture or be a result of the use of very damp clay in nest construction. Open brood cells were not observed during brood development, unlike some other species in the sub-genus (KNERER and PLATEAUX-QUÉNU, 1966). The cells were lined with a waxlike material as is usual in halictines.

A blind ending burrow extended for approximately 5 cm beneath the brood cavity.

L. laticeps has a nest architecture of the subtype OHCib'B according to the classification adopted by SAKAGAMI and MICHENER (1962).

Seasonal cycle

The aggregation was first observed on the 16th of April 1980. At this time the overwintered females flew around the nest site and fed at flowers of *Taraxacum* and *Tussilago*. Pollen collection was not observed.

On May 16th pollen collection was in full swing. The aggregation was observed for several hours on this and the following two days. Out of some twenty nests that were observed, all appeared to be monogynous with the possible exception of one nest where two females were observed to enter the same crack in the soil within a few minutes of one another.

Table I. — Contents of 16 nests of *L. laticeps* excavated on the 25th of June 1980 and containing spring brood. The counts for females refer to workers in both the pupal and adult stages.

Tableau I. — Les contenus de 16 nids de *L. laticeps* déterrés le 25 juin 1980 avec le couvain de printemps. Les données pour les femelles concernent les nymphes et les ouvrières.

	Larvæ	Males	Females	Total
Total	4	30	54	88
Range	0 - 2	0 - 11	0 - 7	3 - 11
Mean per nest	0.25	1.825	3.375	5.4

A summary of the contents of sixteen nests excavated on the 25th of June and containing the spring brood is shown on *table I*. That the first provisioning phase was completed by this date is shown by the complete absence of offspring younger than the full grown larval stage. Contents of the nest with 11 male pupæ indicates that there may be a low frequency of polygyny in this species, as this nest contained twice the average number of cells (mean = 5.4). Including the contents of incompletely excavated nests, the males comprise 23.8 % of the first brood.

Cell clusters containing summer brood were excavated on the 4th and 5th of August and taken back to the laboratory. At this time a few workers

Table II. — Contents of 23 nests of the summer brood of *L. laticeps* excavated on the 5th and 6th of August 1980.Tableau II. — Contenus de 23 nids avec couvain d'été de *L. laticeps* déterrés au cours de la cinquième et la sixième semaines d'août 1980.

	Mouldy	Empty	Larvæ	Male pupæ	Female pupæ	Total
Total	61	94	57	43	18	273
Range	0 - 9	0 - 7	0 - 10	0 - 6	0 - 3	5 - 18
Mean per nest	2.65	4.09	2.48	1.87	0.78	11.87

continued to forage for pollen, largely from *Daucus*, and the overall productivity figures have probably been underestimated as a result (*table II*).

The pupal counts obtained from these nests indicate a preponderance of males in a ratio of 3 : 1 males to females. However, as a result of protandry it is likely that the empty cells would have already produced males and that the cells containing larvæ would have produced female offspring. If these points are taken into account then the estimated sex ratio becomes 2 : 1 males to females. This, however, may still be inaccurate for two reasons — firstly, incomplete and unconstructed cells would probably have produced females, and secondly, the sex ratio of the cells whose contents became mouldy may not have been one to one.

The site of the aggregation was visited on the 30th October 1980 and several holes were dug in the attempt to locate overwintering females. None were found indicating that this species does not hibernate in the natal nest.

Caste differentiation

Females collected from flowers and excavated from nests were dissected to assess their reproductive status; their wing and mandibular wear was noted to give an estimate of their relative age. The head width and wing length of each specimen were measured so that morphological caste differentiation could be investigated.

There is considerable size overlap between the castes (*fig. 2*). The queens being, on average, 4.5 % larger than the workers based upon head width (for queens, mean = 2.07, S.D. = .08, n = 32; for workers, mean = 1.98, S.D. = .08, n = 77) and 7.3 % larger based upon wing length (for queens, mean = 5.43, S.D. = .25, n = 31; for workers, mean = 5.03, S.D. = .24, n = 68) (*fig. 2*).

18 % of the workers collected from flowers or excavated from nests during August were mated (11/61). 53 % of the workers showed some ovarian development but only three individuals had a mature oocyte.

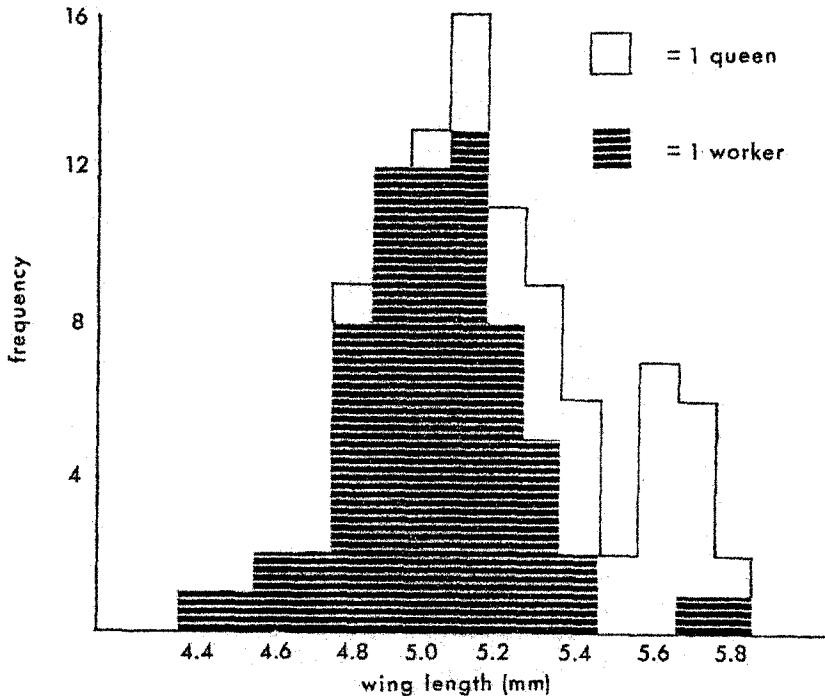


Fig. 2. — Histogram showing size variation in queens and workers of *L. (E.) laticeps*. n for queens = 31, n for workers = 68.

Fig. 2. — Variation de taille chez les reines et les ouvrières de *L. (E.) laticeps*. nb de reines = 31, nb d'ouvrières = 68.

Nest defense and natural enemies

Individual nests of *L. laticeps* are difficult to find due to the friable nature of the soil in which they burrow and the fact that the nest entrances are situated in cracks in the soil. It is not known whether the burrows are actively guarded during the summer provisioning phase. However, when grass stems are placed into burrows or cavities of nests which are in the process of being excavated, females would bite at and attempt to sting the intruding object, and abdominal blocking was elicited.

Several females of *Sphecodes ephippius* were observed flying low over the aggregation during both spring and summer activity phases, and one female of this cleptoparasitic halictid was dug out from a *L. laticeps* nest on August 5th.

Larvæ of the conopid *Thecophora* were found in the abdomens of 10 % of the worker bees collected in August.

Despite the presence of these natural enemies, which are often very damaging to halictine aggregations (KNERER, 1973), it seems that cliff erosion

and land slippage are responsible for a greater proportion of the mortality incurred by this species, being capable of wiping out entire aggregations.

DISCUSSION

Most species of *Lasioglossum* nest in the ground, although some utilise rotting wood or abandoned beetle burrows in wood (STOCKHAMMER, 1967). On the unstable clay cliffs of the south Dorset coast, *L. laticeps* begins its burrows in cracks in the dry surface of otherwise moist clay soil. This is in marked contrast to the preferred entrance sites of *L. malachurum*, where, despite nest densities of over 200 per square metre on the Isle of Wight, not one entrance was found to be situated in a crack. Indeed it seemed that the queens of this species actively avoided cracks in the soil when choosing a nest site, as most entrances were near the centres of patches of soil edged by cracks (unpublished observation). It seems likely that the preference of *L. laticeps* for nesting in cracks serves as a preadaptation for its more unusual choices of nesting in stone walls and cobbled streets. One advantage that nesting in cracks may confer is that it renders the burrow more difficult for cleptoparasites to locate.

Soil nesting halictine bees usually excavate cells at increasingly greater depths as the summer progresses. It is generally accepted that bees avoid cell construction in dry soil, and therefore have to dig deeper later in the year to avoid the drier substrate nearer to the surface (SAKAGAMI and MICHENER, 1962). *L. laticeps* showed a much reduced tendency to dig deeper summer clusters, and in at least two cases these were at the same depth as the spring ones. The reason for this is probably the high moisture content of the soil only a few centimetres beneath the surface at the Charmouth site.

It has been suggested that cavity formation itself is an adaptation to nesting in damp soil as a mechanism to improve drainage and prevent the waterlogging of the soil around the cells (KNERER, 1980). For example, in a particularly heavily watered laboratory nest of *Halictus ligatus*, the queen constructed the cells close together in a cluster and surrounded them with a cavity (PACKER, unpublished observation). This is the first time that this has been observed in this species, despite the fact that hundreds of nests have been excavated by several workers in a wide range of localities. Along with several other species of cluster — making *Lasioglossum*, *L. laticeps* enlarges the cavity as the cell cluster is built up. This may be of particular importance because of the continuously damp nature of the soil at Charmouth.

L. laticeps females, like those of *L. malachurum* (LEGEWIE, 1925; BONELLI, 1948; but see also STÖCKHERT, 1923) do not overwinter in the natal nest. Whereas the gynes of *L. lineare* each constructs a hibernaculum beneath the summer brood cluster of the natal nest (KNERER, 1983). This is an important point

because spring polygynous associations between sisters are only likely to form in those species in which the females overwinter in their natal nest. It is not surprising therefore that *L. lineare* is the only species of the three which regularly forms polygynous associations in spring.

L. laticeps is one of the species of *Evylaeus* which possess a carinate propodeum. This character is shared by many solitary and social species. Those known to be social include *L. pauxillum*, *L. lineare*, *L. malachurum*, *L. calceatum*, *L. nigripes* and *L. duplex*. Preliminary taxonomic studies (PACKER, in progress) indicate that *L. laticeps* is more closely related to the first three species and, therefore, it is with these that its social level will be compared.

BREED (1976) has shown that several characteristics relate to social level in bees of the *Lasioglossum* sub-genus *Dialictus*. He found that the size difference between queen and workers, number of bees per nest, percent seasonal size variation in workers, queen longevity and the number of queens in the nest were the most important factors. In addition, KNERER (1965) has mentioned the proportion of males in the first brood as being particularly important in judging the social level of *Evylaeus* species.

With only one worker brood during the summer, the seasonal size variation of workers in *L. laticeps* cannot be assessed and, as already mentioned, *L. laticeps* appears to be mainly monogynous. However, with respect to the remaining characteristics that are related to social level it is the most primitive species of the *L. malachurum* species group. Thus it has a lower first brood productivity, with a mean of 5.4 offspring per nest as compared to a range from 6 to 8 individuals in the first broods of *L. lineare* and *L. malachurum* (KNERER, 1983) (the mean reported here for *L. laticeps* is probably close to its maximum at this locality because of the unusually good weather during the spring foraging period). With a mean size difference between the castes of only 7 %, 24 % of the first brood consisting of males and with 18 % of the workers being mated and 53 % of them showing some ovarian development, *L. laticeps* is certainly a very primitively eusocial species. As in *L. pauxillum*, the brood cells of this species appear to remain closed, whereas those of *L. malachurum* and *L. lineare* (as well as *L. (E.) marginatum* and *L. (E.) cinctipes*) remain open until pupation to facilitate the removal of dead or diseased larvæ (KNERER and PLATEAUX-QUÉNU, 1966), also indicating a relatively lower level of social organisation for this species.

A comparative behavioural analysis of carinate species of *Evylaeus* is in preparation and should show more clearly the route of social evolution in this group.

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