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# Social evolution and its correlates in bees of the subgenus *Evylaeus* (Hymenoptera; Halictidae)

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**Summary.** Eleven behavioural characteristics of eight species of the subgenus *Evylaeus* were analysed using principal components analysis. The first component axis represents social level and explains over forty percent of the total variation in the data. The following characteristics are highly correlated with social level – (i) a reduction in the proportion of males in the first brood, (ii) a reduction in the proportion of workers that mate, (iii) a reduction in the proportion of workers that have developed ovaries, (iv) an increase in the mean number of workers, (v) increased contact between adults and developing brood and (vi) an increase in the size difference between queens and workers. Because these factors appear, in general, to be under the control of the queen it is argued that parental manipulation has been an important component of social evolution in these bees. The number of worker broods and the mechanism of male production are also related to social level but are less important. Nest architecture, nest defense and polygyny seem to be unrelated to social level. Variation in nest architecture may be in response to edaphic features of the substrate. The lack of any relationship between polygyny and social level implies that the semisocial route to eusociality was not the one taken. It is likely that polygyny can only occur where the substrate is suitable for the winter hibernation of sisters in their natal nest. Multivariate methods are useful in determining the relative social level of closely related halictine species.

## Introduction

Despite the publication of a large number of papers dealing with the social organisation of individual halictine species, our understanding of the origins and further elaboration of sociality in this group remains poor. One reason for this is that the group is taxonomically very difficult and whether two species share sociality by descent from a social common ancestor, or by convergence, is a problem which has yet to be seriously addressed. Furthermore, with the exception of Breed (1976), there has been little serious effort to identify those biological features of halictines which may be used to measure relative social level.

Here we present a multivariate analysis of several biological characteristics for a taxonomically restricted group of halictine bees, in an attempt to identify those features which are most closely related to social evolution and to order the species according to their relative social level. We use principal components analysis because this is a technique which reduces complex data structure into a smaller set of uncorrelated (orthogonal) components and ordinates the objects into the reduced space. Here our objects are species populations of the subgenus *Evylaeus* (genus *Lasioglossum*), and the characteristics are biological attributes which may be related to social evolution.

Principal components analysis has been used to study social evolution in bees on two previous occasions. Michener (1974) analysed 28 characteristics of 18 species of bees from a wide taxonomic spectrum. He found that the species fell into taxonomic and not social groupings. This indicates that the details of social organisation may have their roots in the life cycles and behaviour of the solitary ancestors. Breed (1976) analysed socially relevant data from a more restricted taxonomic range of bees: the subgenus *Dialictus* of *Lasioglossum*. He found that five of eleven characteristics were related to social level and that the resultant multivariate ordination of species agreed well with previous social classifications. However, the species included belong to several species groups (Eickwort, personal communication), amongst which it is likely that social behaviour has evolved several times.

Here we analyse data from eight Old World species from a restricted section of the subgenus *Evylaeus*. These species may be sufficiently closely related for it to be possible that they share sociality by descent from a common eusocial ancestor. A detailed taxonomic study of these species is in progress and the results will be published elsewhere.

## Methods

The biological characteristics used in the principal components analysis are given in Table 1. Unfortunately, data on several important social attributes, such as queen longevity and the mechanism of caste determination, are either completely lacking or are available for only a few of the species under consideration. The relevance of the first six characteristics to social evolution should be obvious from a comparison of solitary and social life cycles. Thus a founding female of a social species would be expected to bias the sex ratio of her first brood in favour of females. She should also increase the number of workers and reduce their reproductive capacity. The latter would be accomplished by inhibiting daughter ovarian development. However, because males are present in the first broods of most of the more primitively eusocial species, and because daughters are more valuable to the queen than granddaughters, she should also reduce the likelihood that her daughters will mate. The workers should be smaller than the queen because smaller bees are cheaper to produce and, presumably, easier to dominate. These five characteristics were included qualitatively by Michener (1974) and, with the exception of the number of workers in the first brood, by Breed (1976).

Further social evolution may result in increased brood care, as shown in some of the species by the existence of open brood cells (Knerer and Plateaux-Quénu 1966), and an increase in the number of worker broods where the climate is favourable (Knerer and Plateaux-Quénu 1967a).

Several additional features have been suggested as being related to social evolution in halictine bees. Breed (1976) found that in *Dialictus* there was a negative relationship between social level and the number of queens in a nest. This may be expected if the evolution of eusociality proceeded via the semisocial route. Thus, polygyny may be more prevalent in the more primitively social species. Improved nest defense has been suggested as a major selective advantage favouring the evolution of social organisation (Lin 1964; Lin and Michener 1972), and it has been suggested that nest architecture has evolved synergistically with sociality (Knerer 1969). Finally, in those species which have the most populous colonies, the number of provision masses made each day exceeds the ovipositional capacity of a single queen. In these cases it seems likely that she allows the workers to lay most of the male eggs thereby increasing total productivity as well as her inclusive fitness (Knerer and Plateaux-Quenu 1967b).

In general, data for the proportion of males and the number of workers in the first brood were obtained from nest censuses around the time of the emergence of the first brood. For species exhibiting polygyny, only the number of workers from monogynous nests were included so that the figures are directly comparable. The reproductive capacities of the workers were assessed by dissection. A worker was considered to have developed ovaries if one or more ovarioles contained a well developed oocyte (state C in Michener and Wille 1966). Mated workers had an opaque, full spermatheca whereas those of unmated individuals were clear and empty. Morphological caste differentiation was measured by the size difference between mean wing lengths of queens and workers, expressed as a percentage of the mean wing length of the queens. Three species have more than one worker brood, at least in some populations. Thus *L. pauxillum*, *L. malachurum* and *L. marginatum* have 2, 1–3 and 4–5 worker broods, respectively. For the multibrooded species, only data concerning the first worker brood is included in our analysis. This is because only first broods are comparable across the complete range of species. However, for the mode of male production, the ovarian development of the last brood of workers was considered (although for most populations there is only one worker brood). This is because it is likely that workers are responsible for laying many of the male eggs only in those populations in which there is considerable ovarian development in the last worker brood (Knerer and Plateaux-Quenu 1967b).

The populations were either mostly polygynous or entirely monogynous with polygyny absent or restricted to a few dubious observations. Only the Dordogne population of *L. lineare* showed a low proportion of nests for which polygyny was definitely established (Knerer 1983). The Japanese population of *L. calceatum* at Okusawa was predicted to be polygynous because of the high frequency of this condition in other populations of this species (Knerer, unpublished observations; Vleugel 1961).

Nest defense was assessed in three categories: nest entrances never guarded, guarded during either the spring or the summer provisioning phase, and guarded during both provisioning phases. Nest architecture varied according to the degree to which the cells were gathered together into a cluster and a cavity excavated around them.

Coding for the last five characteristics in Table 1 are as follows: open cells: 0 = cells closed during larval development, 1 = cells open; polygyny: 0 = nests monogynous in spring, 1 = most nests polygynous; nest defense: 0 = nests unguarded, 1 = nests guarded in either spring or summer, 2 = nests guarded in spring and summer; nest structure: 0 = no cavity around either spring or summer brood cells, 1 = cavity around spring brood only, 2 = cavity around spring and summer broods; male production: 0 = queens lay all or almost all of the male eggs, 1 = workers lay most of the male eggs.

Data are available for eight species of *Evylaeus*: *L. laticeps* (Packer 1983); *L. pauxillum* (Knerer, unpublished observations); *L. lineare*, both localities (Knerer 1983); *L. malachurum*, all localities (Knerer, in preparation); *L. calceatum* (Sakagami and Munakata 1972); *L. duplex* (Sakagami and Hayashida 1960, 1961, 1968; Sakagami and Fukuda 1972); *L. nigripes* (Knerer and Plateaux-Quênu 1970) and *L. marginatum* (Plateaux-Quénu 1959). Other species for which suitable data are available are either only very distantly related (e.g. *L. politum* and *L. glabriusculum*) or are from other continents and details of their taxonomic affinities unknown at present (e.g. *L. cinctipes*).

All of these species have an annual colony cycle with the exception of *L. marginatum*, which is the only known halictine which has perennial colonies, lasting for up to six years (Plateaux-Quénu 1959).

Comparative data for a hypothetical solitary species are included in Table 1. There are in fact several solitary species which are closely related to the species listed in Table 1 (e.g. *L. fulvicorne*) and some of these have been studied, but in insufficient detail (Sakagami and Munakata 1966; Knerer, unpub-

**Table 1.** Raw data for the subgenus *Evylaeus*. *n.a.* data not available

| Species | Locality | % males 1st brood | Mean *n* workers 1st brood | % workers with developed ovaries | % workers mated | % size difference | *n* worker broods | Open cells[a] | Polygyny[a] | Nest defense[a] | Nest structure[a] | Male production[a] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Solitary | – | 60.0 | 0.0 | 100.0 | 100.0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *L. laticeps* | Dorset, England | 23.8 | 4.1 | 53.0 | 18.0 | 7.3 | 1 | 0 | 0 | 1 | 2 | 0 |
| *L. pauxillum* | Tulln, Austria | 5.0 | 4.0 | 15.0 | 1.0 | 14.5 | 2 | 0 | 0 | 1 | 1 | 0 |
| *L. lineare* | Paris, France | 1.0 | 4.1 | 13.6 | 0.5 | 15.0 | 1 | 1 | 1 | 1 | 2 | 0 |
| *L. lineare* | Dordogne, France | 1.5 | 6.3 | 3.2 | 0.5 | 21.0 | 1 | 1 | 0 | 0 | 2 | 0 |
| *L. malachurum* | IOW, England | 2.3 | 6.7 | 3.4 | 0.8 | 14.3 | 1 | 1 | 0 | 1 | 1 | 0 |
| *L. malachurum* | Marseilles, France | 1.3 | 6.8 | 6.8 | 0.0 | 18.0 | 3 | 1 | 0 | 1 | 1 | 1 |
| *L. malachurum* | Dordogne, France | 2.0 | 5.1 | 30.1 | 0.0 | 17.5 | 2.5 | 1 | 0 | 1 | 1 | 1 |
| *L. malachurum* | Estepona, Spain | 1.5 | 6.5 | 17.6 | 0.0 | 18.1 | 2 | 1 | 0 | 1 | 1 | 1 |
| *L. calceatum* | Okusawa, Japan | n.a. | n.a. | 18.6 | 16.3 | 5.0 | 1 | 0[b] | 1[b] | 2[b] | 2[b] | 0 |
| *L. duplex* | Hokkaido, Japan | 10.0 | 4.6 | 20.2 | 8.5 | 9.6 | 1 | 0 | 0 | 1 | 2 | 0 |
| *L. nigripes* | Dordogne, France | 4.0 | 7.2 | 59.0 | 1.0 | 10.3 | 1 | 0 | 1 | 0 | 2 | 1 |
| *L. marginatum* | Dordogne, France | 0.0 | 3.5 | 0.0 | 0.0 | 0.1 | 5 | 1 | 0 | 0 | 0 | 1 |

[a] For explanation of coding for these characteristics, see text
[b] Value predicted from studies on other populations

lished; Eickwort, unpublished). Real data from solitary species such as *Lasioglossum* (*L.*) *leucozonium* and *L.* (*E.*) *oenotherae* indicate that the first brood sex ratio would be male biased (Knerer and Mackay 1969).

The data shown in Table 1 were subjected to a principal components analysis (Tatsuoka 1971; Gates 1983). This is a technique whereby a data matrix can be simplified by a reduction in dimensionality. The resulting dimensions, the principal component axes, represent linear trends amongst the original variables, and one attempts to ascribe their biological meaning from an inspection of the factor loadings of the original characteristics upon the new axes. These factor loadings are correlations between the original variables and the new axes (Gates 1983). The method assumes that the data are multivariate normal and therefore the data were standardised before analysis. The principal factors were extracted from a variance – covariance matrix of the standardised data. The computer program package NT-SYS was used throughout.

## Results

The factor loadings for the first four component axes and the percentage of the total variation explained by each are shown in Table 2. The analysis gives only four significant component axes (those with an eigenvector greater than unity). As can be seen from the factor loading scores, factor one seems to relate to what may be loosely called social level. Thus a reduction in the proportion of males in the first brood and a reduction in the frequency of ovarian development and mating in the workers are accompanied by an increase in the size differ-

**Table 2.** Results of principal components analysis of *Evylaeus* social data

| Variable | Principal component axis | | | |
|---|---|---|---|---|
| | 1 | 2 | 3 | 4 |
| % males in first brood | −0.989 | 0.068 | 0.120 | −0.098 |
| Mean no. of workers in first brood | 0.848 | 0.255 | −0.075 | −0.313 |
| % workers fecund | −0.862 | 0.027 | −0.204 | −0.366 |
| % workers mated | −0.953 | −0.136 | 0.103 | −0.076 |
| Caste size difference | 0.711 | 0.201 | 0.432 | −0.412 |
| No. of worker broods | 0.508 | −0.721 | −0.256 | 0.340 |
| Open brood cells | 0.664 | −0.442 | 0.247 | −0.133 |
| Polygyny | 0.028 | 0.603 | −0.670 | 0.003 |
| Nest defense | 0.239 | 0.523 | 0.120 | 0.614 |
| Nest architecture | 0.269 | 0.889 | −0.079 | −0.149 |
| Male production | 0.441 | −0.575 | −0.514 | −0.264 |
| Eigenvalue | 4.877 | 2.603 | 1.119 | 1.02 |
| Percent explained | 44.34 | 23.67 | 10.17 | 9.27 |
| Cumulative percent | 44.34 | 68.00 | 78.18 | 87.45 |

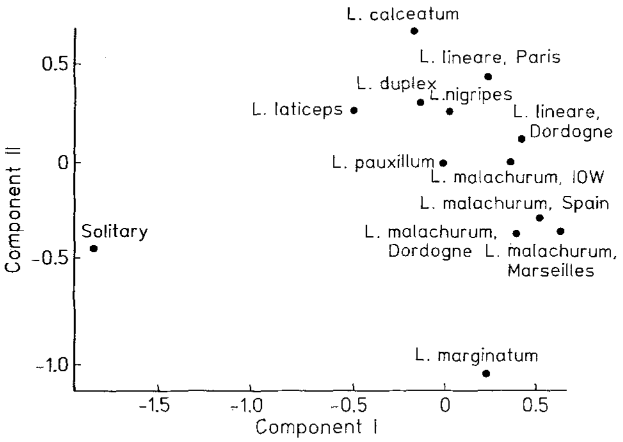

**Fig. 1.** Diagram showing the position of the various species and populations of *Evylaeus* with respect to the first two principal component axes

ence between the castes, an increase in the number of first brood workers and increased contact between adults and developing brood. An increase in the number of worker broods and the development of a worker laid male strategy are somewhat less important in the determination of this axis. This first factor explains over 44% of the total variation in the data. Nest architecture, the number of worker broods, polygyny and male production are the attributes which, in decreasing order of importance, load most heavily upon the second component axis. This axis explains 24% of the total variation. It is not easy to assign a simple biological meaning to this axis. However, the problems associated with the excavation of a cavity around the brood cells increase as the productivity of the colony increases. Similarly, the likelihood that the number of provision masses made will exceed the ovipositional capacity of the queen also increases with productivity, with the result that the workers may lay many of the male eggs in the larger colonies. Thus it is possible that the second axis mainly reflects an increase in the number of worker broods and the results that this has upon nest architecture and male production. Polygyny and a worker-produced male strategy are the attributes which load heavily upon the third axis, which explains ten percent of the variation. The fourth axis explains nine percent of the variation, and nest defense is the only factor with a high loading.

Figure 1 shows the positions of the populations in the two dimensional space resulting from the first two principal component axes. Not surprisingly the hypothetical solitary ancestor lies far to the left of the social species. A gradual increase in social level, along component 1, from the primitive *L. laticeps* to the advanced, but very different, social organisations of *L. malachurum* and *L. marginatum* can be seen.

## Discussion

From Table 2 it can be seen that six characteristics are highly correlated with the first component axis, three are barely related at all and another two are intermediate. We will discuss these three sets of characteristics separately, in increasing order of importance to principal component 1, which we interpret as social level.

Nest architecture, nest defense and polygyny do not appear to be related to social level and thus, alternate explanations must be found to explain the variation in these characteristics.

Nest architecture varies in the species under consideration in the extent to which the cells of worker and reproductive broods are surrounded by a cavity. That the presence of a cavity is not dependent upon the presence of a social organisation in *Evylaeus* is shown by the existence of a complete cavity in the nests of the solitary *L. quebecense* (Eickwort, personal communication). In addition, the socially most advanced species, *L. malachurum*, usually only constructs a cavity around the cells of the first worker brood. Sakagami and Hayashida (1968) suggest that this is because of the problems involved with excavating a cavity around a large cluster of cells containing reproductive brood and supporting it on thin earthen pillars. It seems likely that the excavation of a cavity is an adaptation to nesting in poorly drained soil (Knerer 1980; Packer 1983). However, it is unlikely that correlations between edaphic characteristics of the substrate and the occurrence of a cavity apply when the whole subfamily Halictinae is considered (Sakagami and Michener 1962).

Nest defense was measured by the presence or absence of a guard during the spring and summer provisioning phases. A much better measure of the efficiency of nest defense would be the mortality rates of the brood within nests and of whole colonies. If such data were available, it might show that brood survivorship is enhanced by the presence of a social structure. It is also worth noting that mortality of undefended nests may not have been noticed with the methods of study employed. Thus our results cannot be taken as evidence that improved nest defense was not a factor promoting the evolution of social behaviour in *Evylaeus*.

Polygyny is an important feature in the social structure of bee societies because of its relevance to the route taken in the evolution of eusociality. For halictine bees the semisocial route has been suggested (Lin and Michener 1972). According to this thesis, the evolution of societies composed of co-operating females of the same generation preceded the origin of matrifilial colonies. If this were the case, then it is reasonable to predict that the more primitive species should be more likely to exhibit polygynous spring associations; but no such trend is apparent from our analysis. It should be noted that there is a slight possibility that *L. laticeps* has a low degree of polygyny and therefore the analysis was repeated with this species coded as being polygynous. This increased the factor loading of polygyny on the first axis to −0.152 – still the lowest variable to load on the social level axis, and the remaining factor scores were changed only at the second decimal place. It should also be noted that four nests excavated towards the end of the spring provisioning phase (two in Vienna and two in the Dordogne) were also monogynous (Knerer, unpublished observations).

*L. calceatum*, *L. nigripes* and *L. lineare* are the only species in which polygyny is frequently observed and all three overwinter in their natal nests (Vleugel 1973; Knerer and Plateaux-Quénu 1970; Knerer 1983). Of the remaining species, *L. pauxillum*, *L. laticeps* and some populations of *L. malachurum*, are the only ones known not to overwinter in their nests. Kin selection theory predicts that sisters are more likely to co-operate in brood rearing than are unrelated individuals (Hamilton 1964). It is likely that the bees that overwinter in the same nest are sisters. Thus polygynous associations are more likely to occur in those species which overwinter in their natal nest (Packer 1983). The question now becomes – what selects for the differences in choice of overwintering quarters?

The English populations of *L. laticeps* and *L. malachurum* utilise potentially dangerous substrates as nest sites. The former species nests in cliffs where there are frequent landslides and the latter in flat clay on the coast which is often deluged by sea water during the ravages of a stormy English winter. Of the other species, *L. duplex* is known to overwinter in the natal nest (Sakagami and Fukuda 1972), whereas *L. marginatum* females not only hibernate but also mate in their natal cells within the nest (Plateaux-Quénu 1959). Both of these species are monogynous. The overwintering habits of the other species are not known. Thus the hypothesis that polygyny can only occur in those species which overwinter in their natal nests remains attractive but unproven. Nonetheless, the fact that polygyny appears not to be related to social level in *Evylaeus* indicates that they may have evolved eusociality by the direct route.

The number of worker broods and the existence of a worker-produced male strategy in large colonies are only weakly correlated with social level. The number of worker broods is likely to be limited both by the duration of suitable weather for brood production and by the ability of the queen to control a larger number of workers. *L. malachurum* and *L. marginatum* are the only species in which nest populations become really large. The former increases the number of worker broods where the local climatic conditions are favourable and the latter builds up the worker population over a number of years. In both of these species, the workers in the most populous nests seem to lay many of the male eggs (Knerer and Plateaux-Quénu 1967b). The queens of *L. malachurum* seem to be limited to laying 6 eggs per day – producing one egg per ovariole. Thus, any provision masses in excess of this number are available for worker oviposition. *L. marginatum* queens are not limited in this manner but the vast number of workers in the last year nests must result in the number of pollen balls exceeding the queen's ovipositional capacity.

Thus both an increase in the number of worker broods and the existence of a large number of worker – produced males would seem to rely upon an already fairly advanced social level.

From Table 2 it is apparent that six characteristics are of great importance in assessing the social level of an *Evylaeus* species. In decreasing order of importance they are – (i) a reduction in the proportion of males in the first brood, (ii) a reduction in the percentage of workers that mate, (iii) a reduction in ovarian development of workers, (iv) an increase in the mean number of workers, (v) an increase in the size difference between queens and workers and (vi) an increase in contact between adults and developing brood as shown by the presence of open brood cells.

It could be argued that the percentage of worker females that mate is a direct result of the availability of males. However, this is not necessarily true, because workers may actively repel the advances of males. This has been observed in laboratory colonies of *L. malachurum* in which small, worker females repeatedly pushed away males that were introduced from other cages. Conversely, queens mated many times in the course of one day (unpublished observations). It seems likely that the influence of the queen inhibits worker acceptance of a male during a mating attempt, as has been demonstrated for *L.* (*Dialictus*) *zephyrum* (Greenberg and Buckle 1981).

Sakagami and Hayashida (1968) have argued that the various attributes of social organisation in halictine bees should be considered separately in order to compare the social levels of different species. However, from our analysis it seems clear that multivariate methods provide a good basis for the comparison of social levels amongst closely related species. But what, exactly, does this variation in social level represent?

The factors that relate to social level also represent queen control of the colonies. The queen determines the size and sex of the individuals of the first brood by varying the amount of pollen in the provision mass and by fertilising or not fertilising the egg laid upon it. The queen also determines the number of offspring in the first brood and, probably, also the likelihood that her workers will mate or develop their ovaries. Thus an increase in social level would seem to represent an increase in the queen's ability to control the constitution of the spring brood and to influence the behaviour of her workers. That the socially important characteristics do not show a regular increase with social level indicates that we are dealing with a complex phenomenon which cannot be reduced to a simple genetic model (such as that of Aoki and Moody 1981). Additionally, the queens might be selected to influence different aspects of sociality in different conditions. We would argue that parental manipulation has been an important factor in the evolution of social behaviour in these bees.

The unique social organisation exhibited by *L. marginatum* is of interest. This species is the only perennially social halictine known: the colonies studied by Plateaux-Quênu (1959) lasted for four or five years before producing a brood of reproductives. The caste of an individual female is determined simply by whether it mates or not. Although data concerning caste determination are lacking for all of the remaining species, it is clear that mating does not turn a potential worker into a queen because of the occurrence of mated workers in many nests. In addition to being behaviourally deviant, *L. marginatum* is also morphologically the most divergent of the species included here (Packer and Knerer, in preparation). It is likely that either *L. marginatum* has evolved sociality independently from other *Evylaeus* species or that it diverged from them at an incipient stage in the route to sociality. It is interesting to note that males and females of this species may be found flying together at the same time of year in Israel (Bytinski-Salz and Ebmer 1974) and Jordan (Else, personal communication). This indicates that *L. marginatum* has a very different colony cycle in more southerly latitudes.

Finally we would like to make it clear that, although we believe in the usefulness of describing social bees in terms of their social level, we do not wish to imply that the more primitive species are simply "on the way" to a "higher" social organisation. We would not accept that all sweat bees would have colony cycles similar to honey bees if only they had the time and opportunity to evolve them! At any stage during its evolution, an organism must adapt to the environment that it encounters. Just because we can place a range of species onto a linear sequence of social advancement does not imply that those which appear to be the more primitive are the less well adapted.

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