

## Comparative biological data in two closely related eusocial species: *Evylaeus calceatus* (Scop.) and *Evylaeus albipes* (F.) (Hym., Halictinae)

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**Key words:** Castes, delayed eusociality, non-delayed eusociality, polygyny, social flexibility.

### Summary

Following a brief review of the similarities and differences between the two closely related species, *Evylaeus calceatus* and *E. albipes*, a description of certain biological features common to both species is given:

- the occasional presence of workers among the first-emerged sexuals of the second brood;
  - a short summer collecting phase by the queen which sometimes appears to initiate foraging by the workers;
  - the possibility of a few queens surviving a second overwintering and possibly digging a second-year nest; a trigynous society is described, composed of a second-year egg-layer associated with two first-year auxiliaries, illustrating a case of delayed eusociality.
- Attention is drawn to the social flexibility of the two species and the influence of environmental factors on the social organization.

### Introduction

The halictine bees *Evylaeus calceatus* and *E. albipes* are trans-palearctic species (Ebmer, 1988). *E. calceatus* is very common in France, and much more so than the related species *E. albipes*. They are annual species which may be found sympatrically (Plateaux-Quénu, 1989). They dig cell clusters, surrounded by cavities, in the earth. Like most primitively eusocial species, they produce two discrete broods, the first composed of workers and males, the second of sexuals: future queens and males (Plateaux-Quénu, 1963, 1985, 1989).

Each foundress works alone during the spring: she digs a nest, provisions a few cells and lays one egg on each completed pollen ball. The workers which emerge from these first-brood cells in late spring and summer are statistically smaller than their mothers (Plateaux-Quénu and Plateaux, 1979; Plateaux-Quénu, 1989, 1991); they

soon become active and supply food to the second-brood cells during the summer, while the queen lays eggs on pollen balls heavier than those of the first brood. At this stage, with division of labour between the queen and the workers, the term of society can be used to describe the community. The summer males, hatched at the same time as the workers, mate with them, then die. The sexuals appear in late summer and early autumn. The males mate with the future queens then die before winter. After mating, the future queens overwinter in the natal nest and disperse in spring; each one founds her own nest, but some females form spring polygynous associations.

My purpose is to recapitulate briefly the similarities and differences between these two closely related species, and then to draw attention to certain biological characteristics which illustrate social flexibility in these species.

### Materials and methods

The two species studied were collected in the south-west of France (Dordogne) and near Paris. Both were observed in the field and reared under laboratory conditions, *E. calceatus* since 1960, *E. albipes* since 1983. Several hundreds of nests of *E. calceatus* have been obtained and used in various laboratory observations and experiments. 53 nests of *E. albipes* were dug in rearing cages and their occupants watched continuously during their active flight periods; foundresses were individually marked, as were their emerging daughters. Some foundresses, captured in the field in April at the beginning of the active period, were immediately put into cages. Others, hatched the preceding year under laboratory conditions, overwintered about six months in a refrigerator at 6 °C; they were placed in small cylindrical plastic boxes (height: 10 cm, diameter: 15 cm) previously filled with earth and provided with burrows; overwintered foundresses were then introduced into rearing cages in spring.

A few specimens of *E. calceatus* and *E. albipes* came from the east of France, in the Nancy region; they were collected during the first provisioning phase in spring 1991. A sample of females of *E. albipes* was collected in Switzerland at Le Brassus in September 1989.

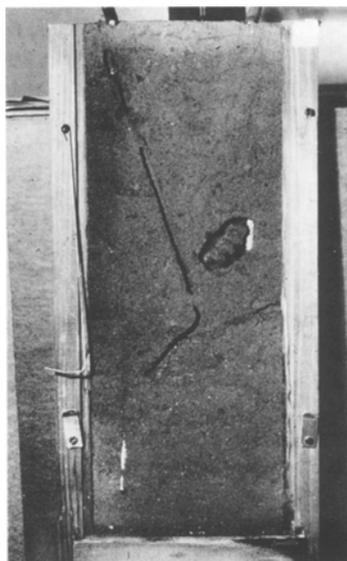
Foundresses of both species were reared in the laboratory under the same ecological conditions.

The rearing cages comprised a flight area and a nesting site made of juxtaposed wooden frames filled with earth (Fig. 1). Each frame was provided with glass panes to allow the inside of the earthen nests to be observed; these observations were fragmentary, lasting, according to the experiments, from 1 to 20 minutes and made possible by a small mirror and an electric torch. Two types of cages were used (Tab. 1).

Two nylon strings were run through the earth in each frame, with the free end dipping into a container filled with water.

Pollen of *Cedrus atlanticus*, *Cirsium eriophorum* and *Salix caprea* was placed on a few artificial flowers and resupplied continuously. A piece of absorbent cotton wool impregnated with diluted honey was placed on another artificial flower.

Light was provided by 18-W neon tubes and 150-W halogen bulbs fitted to the glass ceiling of the cages. The photoperiod was roughly similar to the natural one. It changed with time as shown in Table 2.



**Figure 1.** Wooden frame filled with earth in which a four-cell nest of *Evyllaes calceatus* has been dug (after Plateaux-Quénu 1983)

**Table 1.** Rearing cages used for *Evyllaes calceatus* and *E. albipes*

	Flight area			Frames Length	Thickness	Depth
	Length	Width	Height			
1. Large cages	1 m	1 m	1 m	15 cm	1 cm	37 cm
2. Small cages	70 cm	40 cm	30 cm	26 cm	1 cm	16 cm

**Table 2.** Photoperiod and its changes through the rearing season

Dates	Photophase	Hours
April 1	12.30 h	07.30 to 20.00
April 15	13 h	07.30 to 20.30
May 1	14.30 h	07.00 to 21.30
June 1	16 h	06.30 to 22.30
July 1	16 h	06.30 to 22.30
August 1	15 h	07.00 to 22.00
September 1	13.30 h	07.30 to 21.00
October 1	11.30 h	08.30 to 20.00

Temperatures were measured within the nests, at a depth of 8 cm and at ground level; they varied from morning until night between a lower value (before light) and a higher one (at 6 p.m.); they also varied according to months (Tab. 3).

The statistical test used to compare the size differences between the castes in the two species is the *t* of Student test.

**Table 3.** Temperatures within the nests (at a depth of 8 cm) and at ground surface with their daily and monthly variation through the rearing period

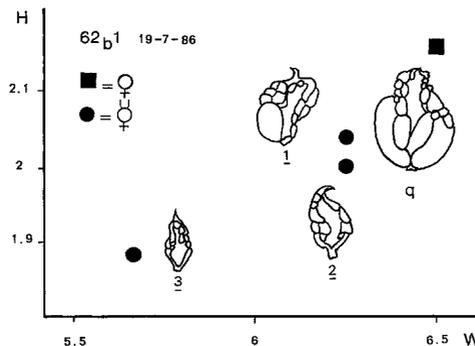
	T within the nests		T on the ground	
	Lower values (°C)	Higher values (°C)	Lower values (°C)	Higher values (°C)
April	16.5 to 19	18.5 to 21.5	17 to 20	25.5 to 28
May	19 to 21	21 to 25	19.5 to 22	28 to 37
June	20 to 22	25 to 27	21 to 22	33 to 37
July	22 to 24.5	27 to 29	22 to 25	34.5 to 37.5
August	23.5 to 25	28 to 30	24.5 to 26	36.5 to 39

## Results

### I. Similarities between the two species

*E. calceatus* and *E. albipes* are similar in various respects.

- *Morphological features.* Both species look alike in terms of external morphology of male and female adults (*E. albipes* is slightly smaller but has a longer face than *E. calceatus*) and male genitalia (Do-Pham et al., 1984).
- *Nest architecture.* The brood cells are always constructed in a comb connected to the main burrow by a short lateral burrow. The cells are built using the same behavioural sequence (Plateaux-Quénu, 1973): they are surrounded by a cavity which grows with the number of cells. The only difference between the nests is the smaller size (length, and especially width) of the *E. albipes* cells, due to the smaller body size of the adults.
- *Biological cycle.* Figure 2 shows clearly that there is only one egg-layer within a summer society of *E. albipes*. Three daughters, the workers 1, 2 and 3 ensured the pollen provisioning of the second-brood cells (Plateaux-Quénu 1989); a division of labour appears regularly in that species as in *E. calceatus* (Plateaux-Quénu, 1963, 1985).



**Figure 2.** Relative size in millimetres (*W*, wing length; *H*, head width) and ovarian development of the members of a summer society of *Evylaeus albipes*. *q*: queen; 1, 2, 3: workers (after Plateaux-Quénu 1989)

The nests of the two species are not guarded, although the head of the queen sometimes appeared at the nest entrance when the workers are absent.

In both species, the workers mate. In laboratory rearing cages, 100% were fertilized. In the field, 85% of a sample of 72 *E. calceatus* workers collected from July 10th to 30th 1984 had mated (Plateaux-Quénu, 1985). Perhaps the last 15% had not yet met with males, which are, of course, much more dispersed in the field than in the enclosed space of a cage.

*E. albipes* workers are particularly attractive to the males, which pounce upon them when they first leave their nests. The female individuals produced in the first brood, even if they mate immediately, start collecting pollen. None of them diapause; they are workers with undeveloped ovaries. The case of *Halictus rubicundus* is quite different: here, females of the first brood that mate when young become diapausing gynes, while those that do not mate promptly become non-gynes and do not diapause even though many mate later (Yanega, 1989).

In both species, as already reported for *E. calceatus* (Torka, 1913; Schremmer, 1955), sleeping groups of males may be seen in the evening at some point of the cage, keeping in contact with one another by the antennae or legs.

Generally monogynous, the two species readily establish polygynous spring societies which form a hierarchy akin to that of a summer society. One female becomes the principal egg-layer, the others or auxiliaries behave as foragers. These polygynous societies may or may not be composed of sisters (Vleugel, 1960). In the first case, the sisters have overwintered in the natal nest. In the second, non-related females join an already dug nest; the closeness of two adjacent nest entrances may sometimes lead to a single digynous nest, as has been observed under laboratory conditions (Plateaux-Quénu, 1973).

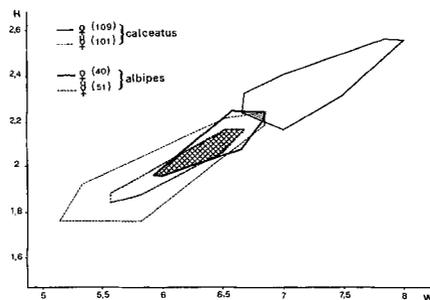
An uncommon case of digyny appeared spontaneously in a cage containing foundresses of both species: a mixed society comprised an *E. calceatus* queen and an *E. albipes* auxiliary doing all the spring pollen collecting (Plateaux-Quénu, 1989). This cohabitation was due to the similar nest architecture of the two species, in which case, mutual tolerance must occur. Direct observation of a definite cell through the glass pane of a frame confirmed that the *albipes* auxiliary worked in common with four newly-hatched *calceatus* workers during the summer provisioning phase. The *calceatus* queen, larger than the *albipes* auxiliary, dominated the latter, and was the sole egg-layer of the society; all the adults produced were *E. calceatus*.

In both species, the brood cells were closed after the egg was laid on the pollen ball. However, they were then reopened, and inspected several times as the brood grew, in both spring and summer nests, by the adult or adults composing the society. I was able to watch this phenomenon directly in my experimental frames, but I am uncertain as to what happens during these visits and whether, as is reported by Batra (1964) for *Lasioglossum zephyrum*, nectar was added to the provisions. The cells containing damaged pollen balls or brood were emptied and filled with soil or destroyed.

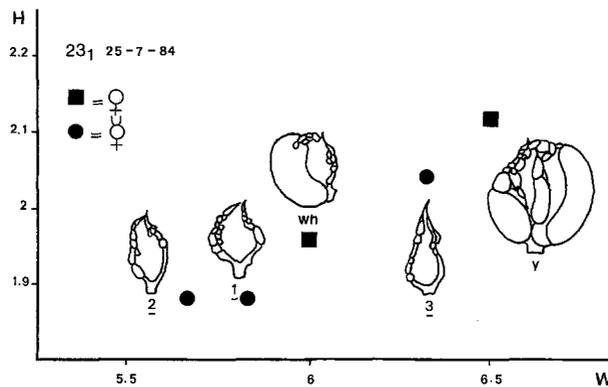
In both species, egg to adult development takes about one month.

## II. Differences between the two species

- *Ecological features.* Certain ecological differences reduce competition between these two sympatric species: *calceatus* forages more frequently on composite flowers and *albipes* on *Ranunculus*. Collecting hours are also different: *calceatus* collects pollen continuously throughout the morning and in the beginning of the afternoon, whereas *albipes* collects pollen early in the morning, then closes the nest and starts again in the afternoon (Plateaux-Quénu 1989).
- *Percentage of males in the first brood.* Both species belong to the many social halictine bees in which small males appear together with the workers. Males were collected in the field, but sex ratios were obtained from laboratory-reared brood censused in the pupal stage. There are more males in the first brood of *E. albipes* (20 to 50% of the total brood) than in that of *E. calceatus* (18% in 22 societies, 14 of them without any male (Plateaux-Quénu and Plateaux, 1980b)). Packer and Knerer (1985) emphasized the importance of the reduction of males in the first brood, a characteristic highly correlated with social level in the subgenus *Evylaeus*.
- *Polyphenism.* Morphological polyphenism is continuous with a large size overlap in *albipes* (Plateaux-Quénu, 1991) and a very small one in *calceatus* (Plateaux-Quénu and Plateaux, 1979) when both species are reared under the same ecological conditions (Fig. 3). Size difference between the castes is 5,6% in *albipes* and 16% in *calceatus*; in both species it is highly significant with  $p < 0.001$  (t of Student test).
- *Digynous nests.* The spring collecting phase stops in digynous societies of *E. calceatus* when a maximum of twelve cells have been completed. It has only been observed to become continuous in a tetragynous society (Plateaux-Quénu 1984): the auxiliaries go on working at least until the appearance of the first worker. In digynous nests of *E. albipes* (6 precise cases of laboratory-reared nests), the pollen-collecting phase is continuous; the auxiliary continues foraging not only until the appearance of the workers but also together with them as soon as they emerge (Plateaux-Quénu, 1989). In Figure 4, the yellow queen (*y*) is the egg-layer; her white auxiliary (*w*) went on provisioning the nest together with the first-brood workers 1, 2 and 3; all four had poorly developed ovaries.



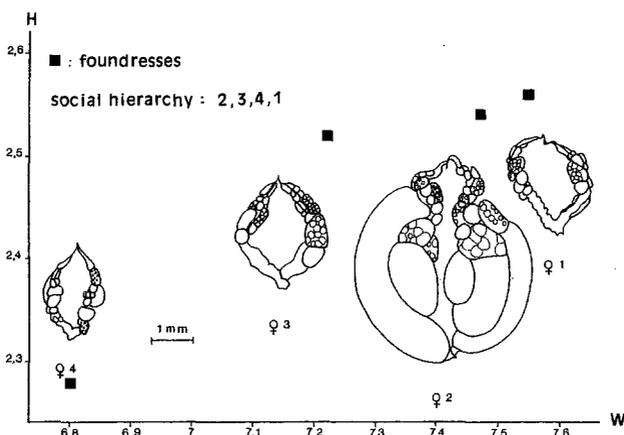
**Figure 3.** Size variation in the two castes of *Evylaeus albipes* (checkered area: size overlap) and *E. calceatus* (stippled area: size overlap). *W*, wing length; *H*, head width, in millimetres. The right-hand areas represent the foundresses, the left-hand areas the workers (after Plateaux-Quénu 1991)



**Figure 4.** Relative size, in millimetres ( $W$ , wing length;  $H$ , head width) and ovarian development of the members of a digynous society of *Evylaeus albipes*. *wh*: white (auxiliary); *y*: yellow (queen); 1, 2, 3: workers (after Plateaux-Quénu 1989)

Only one case of a mixed digynous society of *calceatus* and *albipes* occurred (cf. p. 5), and this led to the following consequences: the *albipes* auxiliary imposed her own rhythm, which was to go on provisioning day after day, after the emergence of the workers. An auxiliary of *calceatus* would have stopped provisioning after a maximum of 12 cells had been completed, then would have shut the nest and possibly provisioned it again later, together with the newly-emerged workers. In this mixed nest, the first brood could not be separated from the second since the activity of the society was continuous. Four workers of *calceatus* emerged among many males; they began collecting pollen together with the *albipes* auxiliary which had not ceased working. Finally, about 15 future *calceatus* foundresses and numerous males were produced in autumn.

- *Polygynous nests.* In polygynous laboratory societies of *calceatus*, the first established foundress in the nest, whatever her size, becomes the egg-layer. Figure 5 illustrates the case of a tetragynous society of *E. calceatus* in which the egg-layer (♀2) was second in size while, paradoxically, the most active forager (♀1) was the largest female (Plateaux-Quénu 1984). Up to now, in polygynous societies of *albipes*, the egg-layer had always been the largest.
- *Orphan worker pupae.* In the same way, a society may arise among grouped worker pupae: in *calceatus*, the egg-layer is the first to emerge even if she is not the largest (Plateaux-Quénu 1979); in *albipes*, up to now, it had always been the largest if she had been the first to emerge (Plateaux-Quénu 1991); a smaller worker appears to be unable to dominate a larger one. Moreover, the ability of grouped workers to produce female brood is evident from a colony of *albipes*: three grouped workers, whose foraging activity was intentionally interrupted after 25 days, produced a brood growing to 6 males and 16 females (73% of female offspring) that emerged in the following order: mmmffmffffm fffffm ffff.
- *Copulation.* The *calceatus* male is almost immobile during mating, after he has pounced upon a female. The *albipes* male repeatedly hits the head and thorax of the female with his antennae and, simultaneously, lifts his wings during copulation.



**Figure 5.** Tetragynous society of *Evylaeus calceatus*. Relative size, in millimetres ( $W$ , wing length;  $H$ , head width) and ovarian development of the four foundresses. ♀2 is the egg-layer, ♀1 is the largest female and the more active forager (after Plateaux-Quénu 1984)

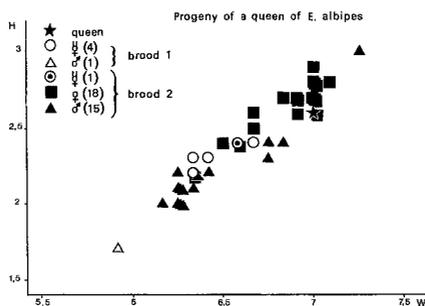
### III. Biological characteristics of both species

- *Occasional presence of workers among the first-emerged sexuals of the second brood.* Yanega (1988) describes an attractive model of intraspecific social diversity in *Halictus rubicundus*. Some mated summer females leave the nest site, undergo a period of diapause and return next spring to dig their own nest. They behave as foundresses instead of workers; they are in fact foundresses produced at the same time as workers.

In four laboratory societies of *calceatus*, a large female which mated and did not share any task in the society appeared among the active workers; these females can be considered as replacement sexuals or as eventual foundresses produced in the first brood (Plateaux-Quénu, 1978). An example of the opposite is again provided by *E. calceatus* and by *E. albipes*, in which I have sometimes observed a few workers emerging with the sexuals of the second brood. One to four *calceatus* workers appeared in a given nest in six specific cases. They generally emerged ahead of the second brood or after a few males. They joined the workers of the first brood and shared in the unfinished pollen provisioning of the second-brood cells.

Similarly, a foundress of *albipes*, whose behaviour was observed daily, produced a first brood of one male and four workers, then a second brood of one worker, 18 future queens and 15 males (Fig. 6). This single second-brood worker foraged together with her four old sisters. She was about the same size as the latter. Two future queens were smaller than her.

- *Summer collecting phase by the queen.* In laboratory-rearing conditions, a short summer-collecting phase by the queen appeared to initiate foraging by the workers. When the workers emerge, the beginning of summer activity starts with the building of a second-brood cell by the queen. In about 30% of the summer



**Figure 6.** Progeny of an *Evylaeus albipes* queen. *W*, wing length; *H*, head width, in millimetres. Note the small size of the only first-brood male. The presence of a second-brood male larger than the future foundresses is unusual

active nests of *E. calceatus*, it is again the queen alone who inaugurates the summer provisioning phase. This may last as long as a week, but ceases as soon as a worker relayed her mother.

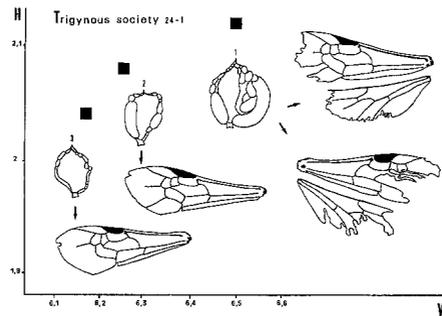
An *albipes* queen collected pollen for two days at the beginning of the summer-provisioning phase, then stayed within her nest and ceased outside work as soon as the first emerged worker had become active.

- *Second-year nests.* A foundress may sometimes survive a second overwintering and dig a second-year nest. Bonelli (1965, 1968) assumed old *E. calceatus* mothers survived until the next spring; later, he abandoned the idea. Among spring females of *calceatus* collected in Okusawa, four were regarded by Sakagami and Munakata (1972) as old mothers having survived for 20–21 months: they had worn mandibles and their ovaries showed previous activity (presence of the corpora lutea). Three of them carried pollen loads on their legs; the fourth had no load but one of her ovaries contained a mature egg. This result suggests that second-year brood production is possible even if it is not frequent.

I have found a few old *calceatus* females among spring foundresses: 1 out of 283 in 1981, 1 out of 54 in 1989. It is difficult to give a meaningful percentage of these rare individuals. In spring 1991, three of them, collected near Nancy, were put into cages; they had yellowish damaged wings and worn pilosity on the thorax. The first, collected on May 9, dug a nest on May 15, but a damaged wing prevented her from flying any more. I dissected her and found well-developed ovaries with a large oocyte. The other two old females, collected on May 9 and May 19, worked alone and provisioned a few brood cells. One produced four males, then two further males one month later. The other produced one male and one worker which remained inactive, inducing her mother to complete two new cells from which males emerged. The old female died on the ground on July 26, having lived 23–24 months.

Certain foundresses of *calceatus* were thus able:

- to overwinter twice
- to show reproductive activity in the second year
- to produce a worker brood
- to survive 23–24 months.



**Figure 7.** Trigynous society of *Evylaeus albipes*. Relative size, in millimetres ( $W$ , wing length;  $H$ , head width), ovarian development and wing wear of the females. ♀1 has overwintered two successive years

Does *E. albipes* show the same characteristics? A few old spring foundresses were collected in the Dordogne and near Paris. In spring 1991, I introduced twelve *E. albipes* foundresses collected on June 2 near Nancy into the same cage; on capture, most of them were gathering pollen. One had severely damaged wings and worn pilosity on the thorax. On June 7, this old female, associated with a younger one, became the egg-layer of a digynous society. On June 13, an adjacent monogynous nest containing a few cells became combined with the digynous nest when the burrows of each nest began to intercommunicate as they enlarged. The resulting nest was trigynous, headed by the old female. I examined this nest on June 19. The old female had well-developed ovaries. She was the egg-layer; her wings resembled lace (Fig. 7). I replaced the frame containing the nest by a new and similar one, and released the two young bees into the cage. They immediately dug a new nest at the very place of the previous one and, on the next day, the larger female had become the egg-layer and the smaller the forager of a new digynous society. Interestingly, the new egg-layer was not the queen of the monogynous nest which combined with the digynous one on June 13: she was the former forager of the digynous nest and the larger of the two remaining bees. This made me think that the size of the females involved plays an important role in establishing the social hierarchy, with the larger female promptly gaining the dominant position. In this example, the old female, nearly two years old, was able to exhibit reproductive activity and produce brood giving rise to adults of both sexes.

## Discussion

*E. calceatus* and *E. albipes* are two closely related species similar in various respects. Certain distinguishing differences (Packer and Knerer 1985) seemed to confer a more primitive eusocial character on *E. albipes*:

- the higher percentage of males in the first brood (20 to 50% instead of 18% in *E. calceatus*);
- the lower value of the morphological polyphenism (5,6% instead of 16% in *E. calceatus*) evident in the large size overlap of the two castes.

I should add to these differences the importance of size in establishing social hierarchy; up to now, in both polygynous spring societies and orphan summer worker societies the egg-layer has always been the largest female. This is not the case for *E. calceatus*, where the first emerged female gains the dominant position.

Similarly, in both species, some workers may appear among the sexuals of the second brood. This shows that sexuals are not necessarily suddenly produced as the result of joint work between a queen and her workers, unless the warm climatic conditions maintained in the rearing cages favoured the appearance of a partial second worker-brood. Some species, *E. pauxillus* and *E. malachurus* in the Paris region, regularly produce two worker-broods before the sexuals are finally produced, and the latter may produce a third worker-brood in the Mediterranean region (Knerer, 1973). We are still unaware of caste determination in these annual species. However, a detailed review on caste induction in halictine bees is given by Michener (1990), who analysed the inhibitory factors preventing some females (workers) from developing into foundresses. Experiments leading to an increase in size of future workers did not change these into functional foundresses (Plateaux-Quénu, 1983, 1988).

The queen's short summer-collecting phase, which frequently appeared in *E. calceatus* and was observed once in *E. albipes*, demonstrated that the newly-acquired role of egg-layer is not necessarily adopted immediately by a queen, who remains able to resume the provisioning of the cells and laying of the eggs as she did during the spring solitary phase. Division of labour occurred either at once, on worker emergence or at a later stage, when, more or less rapidly, workers became active.

Some foundresses of both species may survive a second overwintering, dig a second-year nest and reproduce. Three old queens of *calceatus* in cages worked alone; one of them gave birth to a worker. An old queen of *albipes* became the egg-layer of a trigynous spring society comprising two other young foundresses. Sakagami and Maeta (1989), working on two species of *Ceratina* (Xylocopinae), *C. japonica* and *C. okinawana*, used the term delayed eusociality for polyethism between the mother (queen) and her daughters (workers) in the year following overwintering. The females of our trigynous society of *E. albipes* (one of them about 19 months old and emerging from her second overwintering, and the other two belonging to the next generation, even though they were not the daughters of the first) constituted an example of delayed eusociality. Delayed eusociality is rather similar to semisociality, the three grouped females being foundresses. But its occurrence depends upon the life span of the queen being long. The prolonged life span of females in solitary species is regarded as a precursor of eusocial life. The subfamily Xylocopinae is outstanding in the long life span of adult females, even in solitary species; prolonged life can sometimes extend to more than one year: 16 months in *Braunsapis sauteriella* (Allodapini) (Maeta et al., 1985), two years or even more in some Ceratinini (Sakagami and Laroca, 1971; Sakagami and Maeta, 1977). Some primitively eusocial Halictinae, such as *E. calceatus* and *E. albipes*, seem to have retained this possibility, even if it remains relatively uncommon due to successive deaths. Delayed eusociality remains facultative in *E. albipes*. It has become obligatory in *E. marginatus*, where the societies are perennial, each headed by a queen who survives for 6 years (Plateaux-Quénu, 1959).

The two annual species *E. calceatus* and *E. albipes*, collected in the south-west of France and around Paris, exhibited non-delayed eusociality, their summer societies comprising a queen and her daughters, the workers, among which division of labour occurred.

In halictine bees, a few examples illustrate the coexistence of solitary and non-delayed eusociality within one species. Foundresses of *Augochlorella striata*, studied at the northern limit of their range on Cape Breton island, may produce a mixture of workers and reproductives as a result of their own foraging (Packer, 1990); the species is known to be eusocial in Kansas (Ordway, 1965, 1966). A similar phenomenon is described by Yanega (1988, 1989), who found a production of reproductives along with workers in the same population of *Halictus rubicundus* in New York.

In the subgenus *Evyllaes*, as reported by Sakagami and Munakata (1972), even under conditions of allopatry, the coexistence of solitary nests and non-delayed eusociality within one species is well documented in one case only: *E. calceatus*. There are no workers on Mount Yokotsu (height: 1167 m) where the species is solitary; in Okusawa, some workers appear, but the difference between the castes is 3,5%, and this difference is 5,5% in lowland Hokkaido as a whole. The same species studied in France demonstrated a difference of 8,3% between castes in the field, 12% in cool rearing conditions (nest temperature varying from 14 to 17 °C) and more than 20% in warm conditions (nest temperature varying from 20 to 22 °C) (Plateaux-Quénu and Plateaux 1979, 1980 a).

In *E. albipes*, non-delayed eusociality and delayed eusociality, as described here, did coexist. Whether this species is solitary under certain environmental conditions, owing to absence of the worker caste, is a question I am now examining. Information from northern Germany (von der Heide, personal communication), the phenological graphs of Ebmer (1971) in Austria, the study of a sample of females collected in Switzerland at Le Brassus, and of another one collected in the east of France, all suggest a solitary status. This has yet to be proved and confirmed by laboratory rearings and further field work.

The two species seem to be able to adapt themselves to various situations: possibility for the queen to start the summer provisioning phase; the possible production of workers in the second brood, which help their older worker-sisters in their uncompleted pollen-collecting work; social adaptation to the ecological situation, from solitary to eusocial status with modulation of morphological polyphenism according to temperature (*E. calceatus*) and, for the queens, the facultative prolongation of their life span by another year and entry into a phase of delayed eusociality.

These characteristics illustrate the social flexibility of species which possess a social potential, which may or may not be expressed, able to modify or modulate its expression according to various environmental conditions. What remains to be known is whether the various life cycles are genetically controlled within each population, or reversible according to environmental conditions. Perhaps the differences between solitary and more or less social populations are controlled partly environmentally and partly genetically.

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Received 27 January 1992;

revised 22 March 1992;

accepted 29 April 1992.