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Research article

Population-typical behaviours are retained when eusocial and non-eusocial forms of *Evylaeus albipes* (F.) (Hymenoptera, Halictidae) are reared simultaneously in the laboratory

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Summary. We compare the behaviour of daughters of *Evylaeus albipes* females from eusocial populations from the West of France with those from a non-eusocial population from the East of the country. When non-eusocial population females are placed in the laboratory under day lengths and temperature conditions similar to those experienced by eusocial foundresses under natural conditions, all five produced a brood of males and overwintering daughters with no workers. When 18 nests were initiated by non-eusocial foundresses under short summer daylengths but warmer than normal temperatures, two produced one worker amongst overwintering female and male brood. Both worker-producing non-eusocial females were from the warmest of the eastern localities. When foundresses of the social population are placed under day length conditions typical for the non-eusocial population but with temperature conditions that are intermediate between the two, all five produced at least one worker. Similarly, if the first brood produced by social foundresses is removed, they raise another brood that contains workers whereas non-eusocial population foundresses who have their first brood removed produce a second brood of overwintering females (although one foundress, again from the warmest of the non-eusocial localities, produced one worker in each of two broods, also with males and overwintering females). We conclude that i) non-eusocial foundresses do not readily produce workers under long summer conditions; ii) the lack of worker production by most non-eusocial population females is not because they cannot produce two broods, but because they have a tendency not to produce workers; iii) eusocial population daughters will become active without diapausing in the presence of any other female – even of the closely related *E. calceatus*, unless the first individual to eclose is the smallest and iv) social population foundresses are incapable of producing overwintering females without the help of workers. These data show an interesting combination of flexibility and constraint on social behaviour in these bees.

Key words: Eusocial, photoperiod, temperature, behavioural phenotypes, social evolution, Halictidae.

Introduction

The social variability found within the subfamily Halictinae has made these bees a major focus of research into the factors that promote the origin of eusociality in insects (Michener, 1990). Most genera or subgenera which have been adequately studied contain both social and solitary species (Michener, 1990; Wcislo et al., 1993; Packer, 1997) and intraspecific variation in social behaviour is frequently considerable (Knerer, 1992; Richards and Packer, 1996). Some species exhibit both solitary and eusocial behaviours (sensu Michener, 1974) in different (Sakagami and Munakata, 1972; Plateaux-Quénu, 1993; Eickwort et al., 1996) or even within the same population (Packer, 1990; von der Heide, 1992; Sakagami and Packer, 1994; Field, 1996), thereby potentially providing particularly promising material for investigating social evolution (but see Packer, 1997 and Wcislo and Danforth, 1997). However, no studies have compared the behaviour of bees from solitary and social populations under controlled conditions. Such experimental rearing is necessary to tease out the factors that cause the differences in behaviour. Although the recent literature suggests that most sweat bee researchers consider environmental rather than genetic factors to be of paramount importance

(Michener, 1990; Richards and Packer, 1996; Wcislo, 1997; Yanega, 1997), critical tests remain to be done.

Evylaeus albipes is one of a growing number of halictine species that exhibits both solitary and eusocial behaviours (Plateaux-Quénu, 1993; Packer, 1997). It is eusocial in southwestern France (Plateaux-Quénu, 1989) and solitary in inland localities in France (Plateaux-Quénu, 1993) and Germany (von der Heide, pers. comm.) where nests are initiated later in summer. Many factors may lead to differences in social behaviour between individuals and these may include maternal effects (Roff, 1996) and complex interactions between genes and edaphic and behavioural environments (Wcislo, 1997). Neither of these are simple to take into consideration: maternal effects include those that work through nutritional influences in the egg or the food provided, cytoplasmic effects or more direct behavioural influences of the mother upon offspring whether developing or as adults. Similarly, reaction norms would need to be investigated in order to provide a complete understanding of the influence of a range of environments upon the phenotypic expression of behaviour. Such detailed analyses are beyond the scope of most experimental work with halictids under normal budgetary constraints as it is a full time job to maintain 20 colonies (Greenberg, 1982). Nonetheless, if the facultatively solitary (Wcislo and Danforth, 1997) behaviour of *E. albipes* is a proximal response of a generalised phenotype to short summer conditions then rearing social population bees under short summer conditions should lead to solitary behaviour being expressed. Similarly, perhaps solitary bees become eusocial under long summer conditions.

In this paper we present the results of experiments where individuals of both populations are reared under identical conditions to each other. These were aimed at simulating both long and short season environments to the extent possible with the facilities available. Thus, day length was close to that of the natural environment for each population although temperature was somewhat warmer than experienced by the eastern population in nature. We believe that day length is the more important variable here for the simple reason that it is predictable whereas average temperatures vary considerably among years for the same time of year at the same locality. For example, in the period 1984–1993, average minimum monthly temperatures at Les Eyzies varied between 5.3 and 10.3°C in May, 9.5 and 12.3 °C in June and 11.1 and 14.6 °C in July. Similarly, average monthly maxima in the same period varied between 17.4 and 26.4 °C in May, 22.9 and 26.5 °C in June and 26.1 and 29.8 °C in July (Meteo France, 1994).

Throughout, we use the terms eusocial, semisocial and solitary following the definitions of Michener (1974). Because semisocial behaviour occurs in both populations, we refer to the eastern population as being non-eusocial rather than strictly solitary. We compare behaviours of eastern, non-eusocial bees with those from the west of France where they are eusocial. Consequently, when referring to *E. albipes,* the terms "eastern" and "non-eusocial" are synonyms as are "western" and "eusocial" (or simply "social").

Packer and Taylor (1997) noted two fixed allozyme differences between the Les Eyzies, eusocial population and two non-eusocial ones (Longemer see below, and Oldenburg in northern Germany). However, in the absence of samples from intervening localities (and elsewhere) it would be premature to conclude that the two behavioural forms are specifically distinct. Additionally, mating between the two has been observed in the laboratory, both of western males with eastern females and eastern males with western females. Dissection of three females of the eastern population mated with western males showed the presence of sperm in the spermatheca, no western females mated to eastern males have been dissected. We have not yet attempted to rear offspring of females mated with males from a different population.

Materials and methods

Bee samples

Spring foundresses of *E. albipes* were collected from four different localities in two regions of France: Les Eyzies, Dordogne (44°55′N, 1°0′E, 90 m in altitude) in the southwest; Villers-lès-Nancy, Meurthe et Moselle (48°39′N, 6°07′E, 335 m), Longemer (48°04′N, 6°57′E, 740 m) and La Schlucht (48°03′N, 7°01′E, 1139 m), both in the Vosges, in the east (Fig. 1). Locations of other places from which we have more limited information (see discussion) are also shown in Figure 1. The eastern localities are cooler and have a shorter warm season (Fig. 2) but with its comparatively low altitude, Villers has a climate more similar to the western localities than do any of the other eastern sites sampled. In all areas the flight period of the bees occurs when the median temperature exceeds 10 °C.

Rearing conditions

Bees from both regions were reared in the laboratory in cages comprising a flight area and nest site made of juxtaposed earth-filled frames (see Plateaux-Quénu, 1992 for details). Photoperiods, approximating

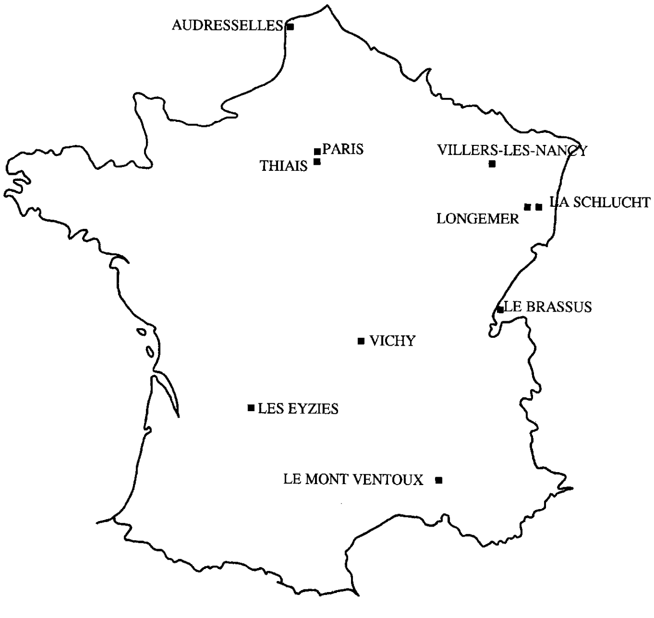

Figure 1. Map of France showing the position of localities mentioned in the text

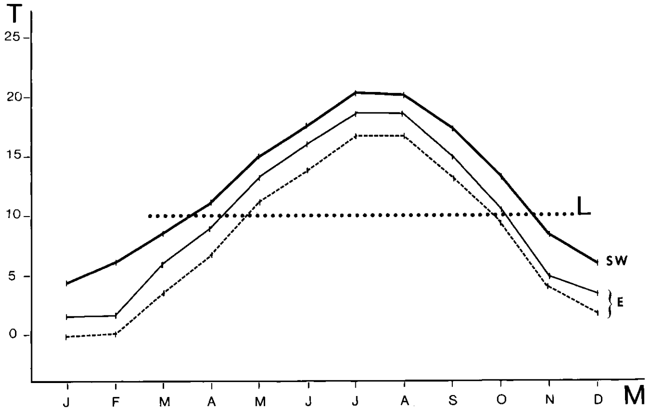

Figure 2. Monthly means of median temperatures (based on the period 1984–1994) for Les Eyzies (SW), and the eastern sites (E), solid line – Nancy, dashed line Gerardmer, near Longemer, altitude 735 metres. The warm season (> 10 °C) is delimited by the horizontal dotted line – L, months – M, temperature °C – T

natural ones for both southwestern and eastern localities, and temperature conditions were as reported earlier (Tables 2 and 3 in Plateaux-Quénu, 1992, respectively). The maximum and minimum temperatures within a month varied by at most 2 °C between years and both were usually within 1° between years, much less than interannual variation in these variables in nature as mean monthly minima and maxima vary for May through July by between 3 and 9 degrees (see introduction).

Some bees used in our experiments were caught in the wild early in the spring (n = 56 for the western population, n = 27 for the eastern population – 22 from Villers, 1 from Longemer and 4 from La Schlucht). All these females were placed either directly in rearing cages (n = 10 from Villers) or refrigerated for a short period of time before being encaged (all remaining females). Four females from Longemer were caught in the autumn and overwintered in a refrigerator at 6°C. Four bees from Les Eyzies, reared from nests in the laboratory the previous summer, were overwintered in a refrigerator after mating. We noted no behavioural differences between individuals resulting from these different protocols.

Determining the caste of laboratory reared daughters

Behavioural differences between worker and overwintering daughters are marked (Plateaux-Quénu, 1989; 1991; 1992; 1993): newly emerged workers are lively and active, quickly learn the location of their nests through orientation flights, feed, mate, fill their natal cell with earth and then help their mother in the construction of new second brood cells and after a few days start collecting pollen. Newly emerged overwintering females are slow and sluggish, feed and mate but do not initiate any digging or pollen collection and eventually enter diapause.

In some cases (n = 35 western population, n = 25 eastern population) emerged female brood were left in the nest with the foundress and their behaviour as a "natural" society observed. In other instances, to control for maternal behavioural effects on the development of worker or overwintering behaviour, the following protocol was used to establish the caste of reared daughters. Reared female pupae (n = 44 western bees, n = 29 eastern ones) were placed in artificial nests (see Fig. 2 in Plateaux-Quénu, 1991). Under these conditions, workers establish small semisocial societies with the subordinate workers becoming active as described above (in addition to the examples described below, we have observed this in 3 pairs of unrelated bees and 8 groups of 3, 3 of sisters, 4 from two different mothers and one in which each bee had a different mother). In these groups, the first bee to eclose was the largest and became the egg-layer in the society except in one instance where the egg-layer was the largest but the second to eclose. When the first bee to eclose was the smallest (n = 3 examples), no society arose: the inactive worker brood bees were unable to enter diapause and died and thus, cannot be considered to be acting as overwintering females. Consequently, we ensured that the oldest pupa placed in a caste-determining nest was not the smallest.

In contrast, with few exceptions (noted below), daughters of non-eusocial population bees behave in exactly the same manner as overwintering females described above (n = 29). This difference in behaviour between non-eusocial and eusocial daughters also clearly appeared when daughters of the two populations were mixed in artificial nests. Two non-eusocial, unrelated daughters remained inactive when grouped with one eusocial population daughter which, alone, became the forager and egg-layer in the nest. One non-eusocial daughter remained inactive when associated with 2 eusocial population females (these 2 were sisters), one of which layed eggs, the other foraged.

Each pupa transferred to a caste-determining test nest was weighed. A combination of weight (and therefore size) differences and individually distinctive paint markings was used to differentiate individuals within nests and ensure that the first eclosing female was not the smallest. Males from other nests were introduced into caste determining nest cages to permit mating which does not influence caste in this species (Plateaux-Quénu and Packer, 1998).

We performed two types of experiments. First, we switched the timing of nest initiation for overwintered females of the two populations such that foundresses were placed in rearing cages under day length conditions typical of the other population. Secondly, we removed the first broods produced by bees from each population.

Day length switching

Diapause duration for foundresses of the non-eusocial population was shortened by removing laboratory overwintered females from the refrigerator earlier than they would emerge from diapause under natural conditions thereby exposing them to day length and temperature conditions typical of the long summer environment of the eusocial population. Dates of encagement varied between March 26th and April 27th (Table 1A). These dates are more than one month earlier than nest initiation and foraging of the eastern population bees in the wild where the first females have been seen in flight on May 2nd in Villers (in 1994) first provisioning on the 17th of the month and most foraging taking place between May 26th and the end of June. Foundresses from the eusocial population were placed under the same rearing conditions simultaneously in cages back-to-back as controls. A total of four experimental and two control nests were set up in this manner (Table 1A). An additional 36 colonies were reared under identical conditions to the 2 control nests but in other years (Plateaux-Quénu, 1989; 1991; 1992; 1993; unpublished).

Diapause of foundresses of the social population was extended by keeping laboratory-reared and overwintered foundresses in the refrigerator for an extended period (n = 2, nests 1 and 2, eusocial population, Table 1B). Additionally, foundresses collected from flowers late in the spring foraging period were placed in cages after two days in the refrigerator (n = 3, nests 3, 4 and 5, eusocial population Table 1B). Under natural conditions western foundresses initiate nests in the last half of April and peak foraging activity occurs in May. Foundresses from the solitary population were placed in cages at a similar time as controls, dates of encagement varied from May 7th to June 14th with a mean Julian date of June 4th (non-eusocial population, Table 1B). All control bees were placed in rearing cages within 24 to 48 h of being captured, with two exceptions that were overwintered in the laboratory (nests 11 and 12, non-eusocial population, Table 1B). As above, three experimental and three control nests were arranged back-to-back. The day lengths experienced by these bees was as expected for non-eusocial bees but the temperature conditions were more similar to those experienced by the western bees under natural conditions because it was not possible to cool the rearing room in a reliable manner. Five experimental and 18 control nests were used.

Table 1. Results of day length switching

Nest	Locality of origin	Date of encagement	Date of 1st provisioning	First brood		Second brood	
				workers	males	females	males
A) Long summer conditions							
Non-eusocial population foundresses, n = 4 (number of males produced not censused)							
1	Longemer	27.iv.92	9.v.92	–	–	2	–
2	Longemer	27.iv.92	11.v.92	–	–	3	–
3	Longemer	26.iii.93	25.iv.93	–	–	1	–
	second brood		5.vi.93	–	–	1	–
4	Longemer	24.iv.93	16.v.93	–	–	3	–
Eusocial population foundresses, n = 38							
1	Les Eyzies	30.iv.92	17.v.92/27.vi.92	2	2	12	12
2	Les Eyzies	26.iii.93	17.iv.93/4.vi.93	1	1	7	8
3–38	Les Eyzies	Data previously presented (Plateaux-Quénu, 1989, 1991, 1992, 1993)					
B) Short summer conditions							
Non-eusocial population foundresses, n = 18							
1	Villers	2.vi.91	9.vi.91	–	–	2	4
2	Villers (3)*	2.vi.91	7.vi.91	–	–	5	8
3	Villers	2.vi.91	7.vi.91	–	–	3	3
4	Villers	2.vi.91	9.vi.91	1	–	2	3
5	Villers	2.vi.91	8.vi.91	–	–	1	3
6	Villers (3)	2.vi.91	7.vi.91	–	–	9	13
7	Villers	2.vi.91	11.vi.91	–	–	1	2
8	Longemer	1.vii.91	3.vii.91	–	–	1	2
9	Villers (4)	8–14.vi.92	15.vi.92	–	–	5	5
10	Villers (2)	11–14.vi.92	19.vi.92	1	–	7	7
11	Villers (2)	7.v.92	23.v.92	–	–	2	2
12	Villers	25.v.92	2.vi.92	–	–	2	3
13	Longemer	5.vi.93	10.vi.93	–	–	1	3
14	Longemer	2.vi.94	7.vi.94	–	–	2	3
	second brood		14.vii.94	–	–	1	2
15	Villers (2)	8.vi.94	14.vi.94	–	–	3	3
16	La Schlucht (2)	2.vi.94	7.vi.94	–	–	5	0
17	La Schlucht	2.vi.94	6.vi.94	–	–	3	2
	second brood		13.vii.94	–	–	1	2
18	La Schlucht	1.vi.94	12.vi.94	–	–	1	0
Eusocial population foundresses, n = 5 (second brood not reared to adulthood)							
1	Les Eyzies	2.vi.88	12.vi.88/19.vii.88	1	2	–	–
2	Les Eyzies	23.v.94	12.vi.94/23.vii.94	1	1	–	–
3	Les Eyzies	25.v.92	1.vi.92/12.vii.92	1	3	–	–
4	Les Eyzies	25.v.92	4.vi.92/19.vii.92	1	3	–	–
5	Les Eyzies	25.v.92	31.v.92/12.vii.92	1	2	–	–

* Number of cofoundresses given in parentheses after locality.

Brood removal

We removed the first brood produced by both eusocial and non-eusocial population foundresses after they had started provisioning at their population-typical time of year. The earth-filled nest frames were removed at least two days after the cessation of foundress provisioning except in the case of two polygynous nests (one from each population) in which foraging was continuous except for the experimental interruption. Broods from both original and replacement nests were reared so that caste could be determined. Three nests of the eusocial population and five of the solitary one were treated in this manner (Table 2).

Results

Day length switching

Data from each nest are presented in Table 1. Under long summer conditions eusocial and non-eusocial population foundresses did not differ in the rapidity with which they initiated foraging after encagement (Mann-Whitney U test, $U = 6$, $p \gg 0.2$). This indicates that long summer conditions do not produce different nest initiation rates between bees of the two populations. Similarly, the Julian date of first provisioning did not differ significantly ($U = 6$, $p \gg 0.2$).

Of the 10 daughters of the four solitary population foundresses, 7 from 3 nests were tested for caste in their natal nest and each remained inactive as is typical for overwintering females. The three daughters from the fourth nest were reared from the pupal stage in the absence of their mother in one caste determining artificial nest. All remained inactive, indicating that continued maternal presence is not necessary to induce daughters to overwinter. In contrast, all 38 eusocial nests produced a brood of workers, 92 in total, 35 of which were tested in their natal nest, 44 in artificial nests and the remaining 13 were used in other experiments (Plateaux-Quénu, unpublished). Thus, 38 social foundresses produced workers and four solitary foundresses produced overwintering females, a statistically significant difference (Fisher's exact test, $p < 0.0001$). Under long summer conditions, one of four non-eusocial foundresses produced a second brood of males and overwintering females (nest 3, Table 1A).

Under short summer conditions the five eusocial population foundresses took an average of 10.3 days to initiate foraging after encagement whereas the 18 non-eusocial form females took 6.8 days (Mann-Whitney U test, $U = 70$, $p < 0.05$). However, Julian dates of first provisioning were not significantly different for bees from the two populations ($U = 59$, $p > 0.2$) indicating that the day lengths experienced during brood production were similar.

Under short summer day lengths each of the 5 western foundresses produced broods containing one or more males and a single worker. One worker was tested in its natal nest, the remainder in artifical nests (3 in the same 3 cell nest, the fourth in a second 3 cell nest with 2 other eusocial form daughters from other rearing cages). In contrast, 18 eastern females produced a total of 57 overwintering daughters and only 2 workers (in 2 different nests, 4 and 10, Table 1B). Conservatively coding the two mixed brood solitary form females as producing workers, the proportion of foundresses producing workers versus overwintering females between the two populations is significantly different (Fisher's exact test, $p = 0.005$, one-tailed as we do not expect solitary females to become eusocial under solitary population photoperiods). Both worker-producing eastern foundresses were from Villers, the most western in climate of all eastern population localities. Two non-eusocial foundresses each produced a second brood of males and overwintering females (nests 14 and 17, Table 1B).

Taken in their entirety, the results from experimental foundresses from both populations were almost exactly the same as if they had been reared under their native environmental photoperiods as control bees. Western population females produced a brood of workers and males, eastern females produced a brood of males and overwintering females, although two of them produced one worker within broods of males and overwintering females and 3 produced two broods of overwintering daughters.

Brood removal

Removal of the first brood of the social form in 3 replicate experiments resulted in another brood of workers and males being produced (Table 2). All of the females were tested in artificial nests; pairs of non-sisters and trios of sisters or of mixed parentage. The effect of removing two successive broods from one society led to workers emerging as late as August 15th whereas under normal laboratory rearing conditions overwintering gynes begin emerging in early July.

Removal of the first brood in 5 replicate experiments with non-eusocial population foundresses resulted in a second brood of males and overwintering females each of which was tested in an artificial nest in pairs of sisters or non-sisters and trios of unrelated bees or as pairs of sisters with one unrelated individual. In one nest (nest 3, non-eusocial population, Table 2) one worker was produced in each brood (along with overwintering females and males).

Discussion

Phenotypes result from complex interactions between genetic and environmental factors. For phenotypes related to solitary and social behaviour, the presence or absence and the behaviour of other individuals when present also form part of the environment (Wcislo, 1997). Consequently, teasing out determinants of phenotypic differences in social behavioural traits is particularly difficult. Although our sample sizes are often small, foundresses were overwintered in two different ways and the caste of daughters was tested in a variety of conditions, our data do permit us to make some conclusions regarding details of the social flexibility of *E. albipes* under laboratory conditions.

First, non-eusocial population foundresses do not readily produce workers when reared under eusocial population temperature and day length conditions. None of the four foundresses so treated produced workers. However, 2 of 18 non-eusocial foundresses produced mixed broods of males, overwintering females and one worker under short summer day lengths but warmer than short summer temperatures. Thus, under conditions typically experienced by eusocial population bees, non-eusocial population foundresses do not simply switch to eusociality. Nonetheless, at least some of the non-eusocial population foundresses have the capacity to produce workers. Interestingly, both of the solitary population foundresses that produced mixed broods of workers and overwintering females came from Villers, the lowest altitude and warmest of the eastern population sources used in our experiments.

Secondly, non-eusocial population foundresses can produce second broods of males and overwintering females under long summer conditions or short summer day lengths but warmer than normal temperatures. This demonstrates that it is not an inability to produce more than one brood of offspring that prevents females of this population from being eusocial, rather it is their tendency not to produce workers that results in solitary behaviour.

Table 2. Results of brood removal experiment

A) Eusocial population foundresses. For each nest the first row represents the data for the first nest, the second row shows data for brood production after the first brood had been removed and for nest 3, the third row shows data for the brood after the second brood had been removed.

Nest	Locality	Date of encagement	Date of 1st provisioning	First brood		Replacement brood		Date of brood removal
				workers	males	females	males	
1	Les Eyzies	9.iv.90	24.iv.90	2	2	0	0	7.v.90
			11.v.90	2	1	0	0	
2	Les Eyzies	27.iv.94	14.v.94	2	2	0	0	17.vi.94
			20.vi.94	2	1	0	0	
3 [a]	Les Eyzies	26.iv.94	10.v.94	4	13	0	0	14.vi.94
			17.vi.94	12	8	0	0	15.vii.94
			18.vii.94	2	3	0	0	
B) Non-eusocial population foundresses.								
1	Villers	2.vi.91	9.vi.91	0	0	2	4	27.vi.91
			11.vii.91	0	0	2	3	
2	Villers	2.vi.91	7.vi.91	0	0	3	3	20.vi.91
			23.vi.91	0	0	1	4	
3	Villers	2.vi.91	8.vi.91	1	0	2	3	20.vi.91
			25.vi.91	1	0	2	2	
4	Villers	2.vi.91	8.vi.91	0	0	1	3	22.vi.91
			25.vi.91	0	0	0	4	
5 [b]	Villers	2.vi.91	7.vi.91	0	0	5	8	27.vi.91
			29.vi.91	0	0	3	2	

[a] This nest was initiated by two foundresses, a third one joined the nest on 15.vi.94 after the first brood had been removed, all other nests had one foundress.

[b] This nest contained three foundresses, all other nests had one foundress.

Third, daughters of the eusocial form will become active as foraging workers in the presence of their mother, even if they are single workers (n = 3 from les Eyzies, n = 4 from Paris and n = 1 from Audresselles), but more importantly, also in her absence as long as there is at least one other female in the nest and the first to eclose is not the smallest. In these cases, the larger individual becomes an egg-laying worker, the other(s) forage(s). This happens when the bees are sisters (n = 3 trios), not sisters (n = 6 pairs, n = 1 trio), when in the presence of one sister and an unrelated individual (n = 4), as groups of three unrelated individuals (n = 2), when a eusocial population daughter is in the presence of a non-eusocial population daughter female (n = 2) and even in the presence of a worker of the closely related species *E. calceatus* (n = 3). Given that functioning societies do not form if the first individual to eclose is the smallest, it would be interesting to have field data on the relative sizes and sequence of emergence of eusocial population brood. Our laboratory experiments lead us to predict that foundresses of the eusocial population do not produce first broods in which the first daughter is the smallest.

Fourth, eusocial foundresses never produce overwintering daughters without the assistance of workers. This fact was demonstrated both in the day length switching and brood removal experiments. This is in contrast to the situation in *Halictus rubicundus* and *Augochlorella striata* in which foundresses can produce overwintering daughters and workers in the same brood (Yanega, 1989; Packer, 1990).

To us, the combination of the first and fourth conclusions above is suggestive of a genetic contribution to the behavioural differences observed between populations. *Evylaeus albipes* foundresses from non-eusocial populations retain their population specific behaviours when reared under controlled laboratory conditions aimed at mimicking, to the extent that our facilities allowed, the natural conditions of the eusocial population. Similarly, eusocial bees remain eusocial under short summer laboratory conditions. This suggests that simple responses to the edaphic environment are not the cause of the behavioural differences we have observed. Concluding that there is a genetic basis to social behavioural differences is not without precedent for complex aspects of social organisation in the Hymenoptera (e.g. Ross and Keller, 1998). For viewpoints stressing the role of environmental variation in causing differences in social organisation, see Richards and Packer (1996), Wcislo (1997) and Yanega (1997). Clearly, more detailed experimentation, including rearing the offspring of controlled crossings through multiple generations is required to firmly establish the basis of behavioural differences among *E. albipes* females.

The social context does have some influence on behaviour, at least for the daughters of the eusocial population. In three cases reported earlier (Plateaux-Quénu, 1991), eusocial population worker brood daughters placed in artificial nests solitarily did not become active and died in autumn, unable to enter diapause as to typical overwintering females. Similarly, we noted above the three instances in which among 2 or 3 social form pupae the first bee to eclose was the smallest. Such groupings did not become semisocial but instead the females were inactive like overwintering females, suggesting that orphaned workers form semisocial societies only when reproductive dominance of the oldest bee is not inhibited by its small size. Additionally, single worker brood daughters become active as follows: i) in the presence of their mother (n = 3 from Les Eyzies, n = 4 from Paris and n = 1 from Audresselles), ii) in the presence of another worker of the same species (3 trios of sisters, 6 pairs and one trio of non-sisters), iii) in the presence of one worker brood female of a closely related species (n = 3) and iv) in the presence of two inactive solitary form conspecific females (n = 2). This suggests the possibility that the presence of almost any other individual adult (solitary or social, parental generation or young daughter, conspecific or sibling species) will induce a single eusocial population worker brood female to become active like a worker.

At present we do not know the geographic limits of the eusocial and non-eusocial forms of *E. albipes*. However, we take this opportunity to list what we do know of the behaviour of other populations. Ten of 11 foundresses obtained from Thiais, near Paris, reared worker daughters and males in the first brood, the remaining female produced a brood of males and overwintering females. Ten foundresses from Audresselles on the coast of northern France, each produced a first brood of workers and males. The species is solitary in Le Brassus (Switzerland) (Plateaux-Quénu, unpubl. obs.); Linz, Austria (based upon the abundance curves of Ebmer (1971)) and at Le Mont Serein (at 1400 m, on the northern slope of Le Mont Ventoux) (Desmier de Chenon's private collection and Plateaux-Quénu and Plateaux, unpubl. obs.). In Northern Germany, the species is largely solitary though a few workers have been observed (von der Heide, pers. comm.). Thus, it appears that, among these localities, the social form is restricted to the warmer, lowland regions of western France and the non-eusocial form is found further inland and/or at higher altitude.

The closest relative of *E. albipes* is *E. calceatus* (Do Pham et al., 1984; Plateaux-Quénu, 1989, 1992; Packer, 1991; Taylor, 1994). Both species are known to be behaviourally polymorphic (Sakagami and Munakata, 1972; Plateaux-Quénu, 1993; Field, 1996). A population of *E. calceatus* sympatric with the non-eusocial form of *E. albipes* in and around Villers in eastern France is eusocial (Plateaux-Quénu, unpubl. obs.). Foundresses of *E. calceatus* here initiate nests one month earlier than those of *E. albipes* and workers have been observed as early as June 23rd. In the laboratory, 13 foundresses of *E. calceatus* from this region each produced eusocial societies. These data demonstrate that the environmental conditions constraining *E. albipes* to be non-eusocial in eastern France do not hold for its sibling species in sympatry.

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