

## **Ontogeny of queen attraction to workers in the ant *Cataglyphis cursor* (Hymenoptera: Formicidae)**

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### **Summary**

The behaviour of *Cataglyphis cursor* workers towards queens at 15 days, one month or two months after worker emergence was tested. Workers reared entirely with their own maternal queen were tested with this queen or with an unfamiliar alien queen. Workers transferred within 48 h of emerging to a new definitive nest with an alien queen were tested with this queen or with the original maternal queen. The degree of attraction to each of these queens and the workers' behavioural repertoire were measured and analysed. The results showed the following: 1) The attractiveness of queens and the workers' queen recognition behaviour were linked. 2) Although unfamiliar alien queens hardly attract workers, familiar alien queens were as attractive as maternal queens, and induced the same strongly marked and unique worker response, indicating that workers learn queen attractant cues in the days immediately after emergence. 3) Agonistic reactions were observed, but workers continued to be attracted to their maternal queen even after developing an attraction response to an alien queen with which they had been reared. These results agree with the proposal that queens produce two kinds of pheromones, those that attract workers and those that mediate recognition of queens by workers. These results show the ability of workers to discriminate between queens. Workers are attracted to any queen, but recognize as nestmates only maternal or alien queens with which they have been maintained. 4) The differential in worker attraction and recognition from 15 days to 2 months and its modifications by post-imaginal experience illustrate worker behavioural ontogeny, which is a basis of social discrimination.

### **Introduction**

The fundamental characteristics of structurally stable societies are the forces promoting cohesion and the integration of individual behaviour. These characteristics gave rise to the "superorganism" concept (Wheeler, 1928; Emerson, 1938) as the feature distinguishing true societies from aggregations of individuals merely occupying the same space.

In colonies of social insects, the queen should be able to attract workers, and so facilitate communication between individuals. Stumper (1956) remarked that attraction of workers by the queen is manifested in three frequently observed phenomena: worker aggregation around the queen, persistent worker licking and grooming of the queen's body, and worker transport of the queen if there is the slightest disturbance. Mediation of these responses is generally thought to be by pheromones. Many investigations demonstrate that some pheromones appear to act by affecting the behaviour of workers, the target individuals, by promoting attraction (Stumper, 1956; Delage, 1968). A specific attractant queen pheromone was first reported in six species of army ants by Watkins and Cole (1966). Jouvenaz et al. (1974) used the same experimental procedure in a study of fire ants. Test papers on which queens of either *Solenopsis invicta* or *Solenopsis geminata* had been confined were attractive to workers. The workers' behavioural response to the queen pheromone was strongly marked and unique. These authors showed that workers respond to non-volatile chemicals, but they did not establish whether volatile attractants were also involved. Vander Meer et al. (1980), however, using an olfactometer, demonstrated that *S. invicta* queens secrete volatile chemicals that attract workers. Comparison of results from bioassays of extracts of mated queens and of other castes suggest that *S. invicta* queens produce an attractant recognition pheromone (Glancey, 1980). Fowler and Roberts (1982) also demonstrated a queen attractant pheromone in *Camponotus*. Brian (1973), analysing "the means by which queens of *Myrmica* communicate their presence to workers' thought that the abdomen is the most likely source of a substance, the emission of which must vary seasonally". Keller and Passera (1989) observed, discussed and stated how attraction and recognition can be distinguished in *Iridomyrmex humilis*.

In *Cataglyphis cursor*, queen attraction substances seem to be identical with colony odour (Berton, 1989), which is not the general rule. *Solenopsis invicta* workers respond as strongly to *S. geminata* queen secretions as to those of conspecific queens (Jouvenaz et al., 1974). There was no reciprocal response of *S. geminata* to *S. invicta* queens. Our recent research (Berton, 1989) shows that *Cataglyphis cursor* workers were not attracted to the nest itself unless it contained a closely related queen, i.e. collected from a society of the same geographic territory (less than 20 kilometres apart). The nest was not made attractive by the presence of an alien, unfamiliar queen.

In certain uncommon circumstances, differences in the social experience of young and older workers can induce great variation in their behaviour (Berton, 1989; Berton et al., 1989). In this study, we investigated the dependence of the worker response to queen attraction on learning. During the immediate post-emergence period of life, workers might develop orientations to cues from new, unfamiliar queens. Attraction to unfamiliar queens could be developed after exposure to chemical cues from such queens. We analysed whether the response to a maternal familiar queen could be altered by post-imaginal familiarization with an alien queen after removal of the original maternal queen. Young workers were tested against the maternal queen, against alien queens to which the workers had been familiarized, or against alien queens with which the workers were completely

unfamiliar. We tested the capacity of workers to be attracted by these queens and the development of the worker's behavioural repertoire.

Our study forms part of an extensive programme of comparative research on the stimuli produced by queens, workers and brood at different stages of development.

## Materials and Methods

### *Rearing*

*Cataglyphis cursor* Fonsc. is a monogynous formicine ant unusual in that it displays thelytokous parthenogenesis (Cagniant, 1973). Samples of this species were collected from different localities in the south of France (Var, Hérault and Pyrénées-Orientales, all being Departments on the Mediterranean coast) to increase the variability of the experimental material. Worker pupae were allowed to mature in the maternal society so that new workers emerged with the help of older ones. All the test colonies were maintained under the same conditions. The ants were reared in the laboratory in an air-conditioned room at  $25 \pm 1.5^\circ\text{C}$  and a constant light regime of L:D = 12 h:12 h from June to September. Hibernation was induced from October until March. Dilute honey and insects were provided daily as food. Feeding continued right up to the beginning of the experiments, so that the influence of hunger on behaviour could be reduced as much as possible.

### *Apparatus*

Experiments were carried out in a rectangular arena of  $170 \times 105 \times 80$  mm. The upper 30 mm of the vertical sides was covered with fluon, which prevented the worker ants from escaping. The arena was divided by reference marks into four equal areas, in each of which was glued a tube. The tubes were isolated from the rest of the arena by gauze, which prevented physical access but allowed some worker antennal contact. The diffusion of any possible volatile compounds would not have been impeded by the gauze. Each of the four areas hence consisted of two surfaces of very unequal area; the gauze and the floor of the area. The area of the floor was about 100 times that of the gauze.

### Experiments

All behavioural observations were carried out between 10.00 a.m. and 3.00 p.m. (local sun time) in an air-conditioned room at  $25 \pm 1.5^\circ\text{C}$ . The only lighting was provided by a ceiling lamp directly overhead.

Two experimental series were carried out between July and October 1986. For each experiment, workers from three different colonies and alien queens from three other different colonies were used. Observations were made on workers at 15 days, one month, or two months after emergence. Newly emerged workers were largely inactive and so were not tested.

### *Experiment 1*

Workers reared entirely with their own queen were tested against

A: their own maternal queen (Control) or

B: an unfamiliar alien queen (with which the workers had no previous contact).

### *Experiment 2*

Workers were transferred within 48 h of emergence to a new nest and reared permanently with an alien unfamiliar queen. Throughout this familiarization period, the queen could be regarded as having been adopted by the workers. The newly constituted societies were reared as described above. The workers were tested against

C: their own maternal queen (from which the workers had earlier been removed) or

D: the familiar alien queen of the new nest.

#### 1. Tests of attraction

For each test, ten workers were taken at random from a single colony and placed at the centre of the apparatus. Three other workers were taken from the same colony and individually confined, one in each of three of the four tubes. The fourth tube contained a queen *C. cursor*. This queen was either the workers' maternal queen, a familiar alien queen or an unfamiliar alien queen.

Queen attraction is defined as the movement of workers toward the queen's volatile odours.

By observation of the 10 workers placed at the centre of the apparatus we were able to identify a repertoire of distinguishable behavioural acts that are mutually exclusive. Each behaviour was defined by three criteria: type (see Fig. 1), location (on the "gauze" or on the outside, the "sides"), and compartment (that containing the queen or those containing isolated workers). The maximum number of behavioural criteria was 28. These data were recorded every five minutes for one hour (thus 12 times for a total of 120 records).

For each group (A to D) three replicates using different societies were made.

The individuals (queen, workers) were not marked, so the ten workers were watched as a group.

#### 2. Tests of aggression

Worker aggression towards the different kinds of queen was assessed. After each series of attraction tests, the queen was removed and placed in a cylindrical cage (80 mm × 50 mm high) free of any queen or worker odour cues. The upper 30 mm of the side was covered with fluon. The 10 workers from the same series were dropped carefully into the cage with the queen, one each minute. An attack was recorded as soon as the first agonistic behaviour was seen, and the test was immediately stopped. In the absence of any aggression the test was continued until all 10 workers had been deposited in the cage, giving a maximum test duration of 10 minutes.

#### 3. Statistical analyses (Siegel, 1956)

Independent group comparisons were carried out, using raw data of each replicate, by Mann-Whitney *U* (one-tailed) tests (significance set at  $P = 0.05$  for  $n_1 = n_2 = 3$ ,  $U = 0$ ) and  $X^2$  tests (bilateral with  $df = 2$ ). Paired group compari-

**Table 1.** Frequencies of some behavioural parameters for *Cataglyphis cursor* workers at 15 days, one month, or two months after emergence, tested against different queen types

	Experiment 1						Experiment 2					
	A			B			C			D		
Age	15 d	1 m	2 m	15 d	1 m	2 m	15 d	1 m	2 m	15 d	1 m	2 m
ACLITRO %	1.67	3.33	4.74	0	6.67	3.61	1.11	7.5	5.29	5.56	1.67	3.33
GRO %	0.83	3.05	2.77	0	8.61	6.11	0.28	4.39	0.56	2.22	1.67	3.61
IMM %	93.06	38.89	33.61	99.72	47.78	47.22	90.56	59.47	48.85	77.22	56.1	33.33
MOV %	3.33	12.78	15	0.28	16.94	10.83	7.22	12.22	10.56	3.61	16.39	11.94
QG %	0.83	20.83	32.22	0	4.17	6.39	0.83	12.22	31.94	0.28	11.11	35
WG %	0.28	21.11	11.67	0	15.83	25.83	0	4.17	2.78	11.11	13.06	12.78
Rep °	5	10.33	11.33	1.33	11	10.67	1.67	10	12	6.67	9	14
Wag	—	—	—	—	1/3	2/3	—	1/3	2/3	—	—	—

A. Workers reared with maternal queen, tested with maternal queen

B. Workers reared with maternal queen, tested with unfamiliar alien queen

C. Workers transferred just after emergence and maintained permanently with an alien queen, tested with the original maternal queen

D. As for C., but tested with the familiar alien queen to which they had been transferred

ACLITRO = Combined data for antennal contacts, licking and trophallaxis recorded on sides

GRO = Grooming on sides

IMM = Immobility on sides

MOV = Moving on sides

QG, WG = Queen gauze and worker gauze respectively

Rep = Number of different behavioural acts in repertoire

Wag = Worker aggressiveness

% = Relative mean frequency

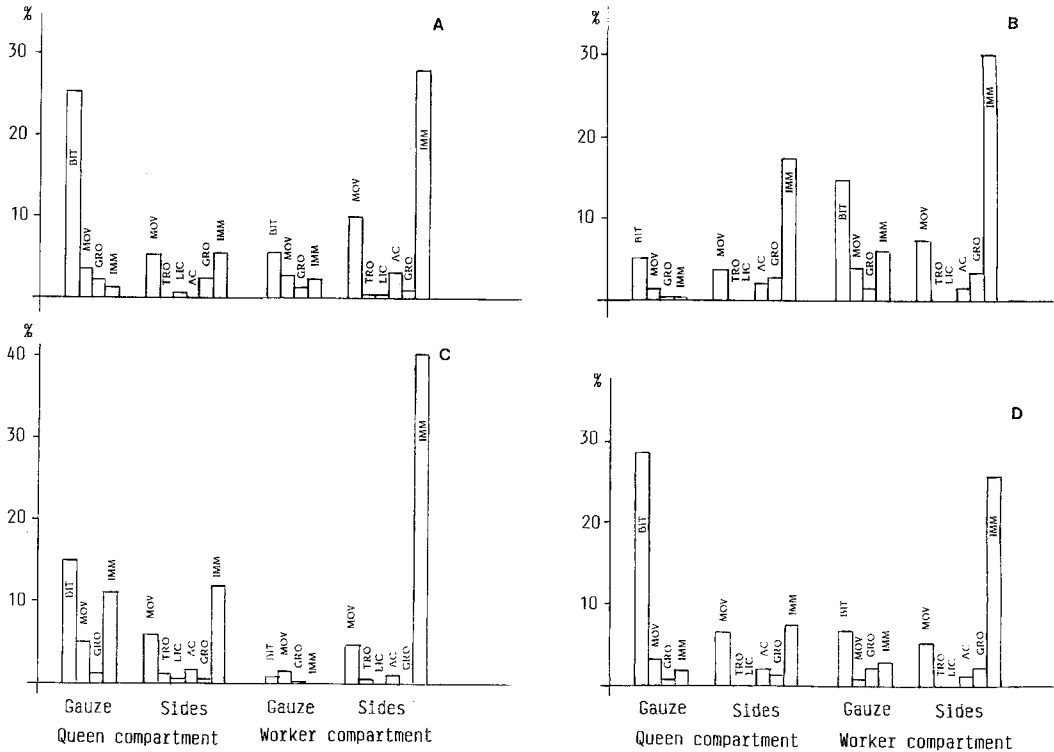
° = Mean frequency

sons were made using 1. Friedman two-way analysis of variance by ranks to test the subject scores dependence of the conditions (such as aging) and 2. the randomization test for matched pairs. In order to give more information and to be more explicit in the presentation of the text, means or relative mean frequencies (percentages of records) are given in Table 1.

## Results

### 1) Experiment 1: (Tab. 1, A/B). Behavioural changes with age in workers (A) and (B) reared with their own queen.

At 15 days after emergence, workers were largely immobile, frequently congregating in the arena. Movement was consequently rare. Antennal contacts, licking and trophallaxis grouped together were rare or even absent, as was self-grooming. The behavioural repertoire was limited. There were very few visits by workers to the pieces of gauze surrounding the tubes containing workers or queens. No aggression was recorded of workers against queens.



**Figure 1.** Description of locations and frequencies of behaviour recorded in tests of *Cataglyphis cursor* workers. Workers reared entirely with their maternal queen: A. tested with the maternal queen. B. tested with an unfamiliar alien queen; workers transferred just after emergence and maintained permanently with an alien queen: C. tested with the original maternal queen. D. tested with the familiar alien queen to which they had been transferred

AC Antennal Contact  
 BIT BITE of the gauze  
 GRO Self-GROOming  
 IMM IMMobility  
 LIC LICKing  
 MOV MOVing  
 TRO TROphallaxis

At one month after emergence, workers were significantly more active and consequently much more mobile than younger workers. There were no significant increases in the frequencies of antennal contacts, licking and trophallaxis. The repertoire of behaviour was greatly increased (significantly). Both the queen and worker gauzes were visited significantly more frequently by workers of this age compared with younger workers. Agonistic behaviour was observed in one out of three tests with the unfamiliar alien queen (B), but in none of the tests with the maternal queen (A).

At two months after emergence, compared with 1 month, there were no significant increases in any of the behavioural categories. However, workers (A) were

frequently observed on the gauze surrounding the maternal queen, and in tests (B) with the unfamiliar alien queen, movement on the arena floor was less frequent. Obvious agonistic behaviour against the alien queen was observed in two out of three tests.

The changes in frequency of immobility and movement in the arena (Friedman two-way analysis of variance by ranks) reflected to some extent the development of the behavioural repertoire in workers at 15 days and 1 month after emergence. The decrease in these measures for 2-month-old workers reflected the richer repertoire of these ants (Fig. 1, A/B).

### *Comparison A/B*

Two-month-old workers (B) seldom visited the gauze surrounding an unfamiliar alien queen, concentrating their visits on worker gauzes ( $P < 0.0001$ ). In tests (A) with the maternal queen, however, the reciprocal situation existed ( $P < 0.0001$ ); visits to the queen gauze were more frequent than those to gauzes surrounding workers (Fig. 1, A/B).

The behaviour of workers at 1 and 2 months towards maternal and unfamiliar alien queens indicated that the frequency of visits to the queen gauze was an accurate means of distinguishing the two situations (1 month,  $P < 0.0001$ ; 2 months,  $P < 0.0001$ ). The maternal queen was more attractive than the alien queen.

The ants enclosed in tubes were inconspicuous, and about 50 mm away from the workers released in the centre of the apparatus. However, the workers rapidly locate the queen, especially at 2 months old, suggesting that they can orientate at long range and/or the queen produces volatile cues. Workers are attracted to queens, familiar or unfamiliar. They contact the gauze but stay to be counted only if they have been conditioned to the queen behind the gauze. Thus, the counts are highest in situations where the workers are familiar with the queen, the maternal queen.

Alien queens provoked worker aggression, but the familiar maternal queens did not. Worker aggression towards queens increased with worker age only in the tests with alien queens. Workers are attracted to any queen, but recognize as nestmate only the maternal queen. These tests confirm that queen attractant power and worker recognition of queens are connected.

### 2) *Experiment 2: Behavioural changes with age, and comparison of worker behaviour towards reintroduced maternal queens (C) and familiar alien queens (D) (Tab. 1, C/D).*

At 15 days of age, there were significant differences between the two groups of workers in the frequency of most types of behaviour tested. In particular, immobility on worker gauzes ( $P < 0.0001$ ) and worker sides ( $P < 0.01$ ) and moving were rarer ( $P < 0.05$ ) among workers responding to a familiar alien queen. Their behavioural repertoire in the queen compartment ( $P < 0.05$ ) was correspondingly greater. Antennal contacts, licking and trophallaxis were more frequent ( $P < 0.01$ ). These ants (D) also made significantly more visits to the worker

gauzes ( $P < 0.0001$ ). These results indicate that, compared with the reintroduced maternal queen, a familiar alien queen promotes worker activity.

At one and two months after emergence the difference between the two groups became less marked. However, there continued to be more movements in group (D) workers (1 month,  $P < 0.05$ ; 2 months, not significant) and consequently less immobility on the sides (1 month, not significant; 2 months,  $P < 0.01$ ). These workers also bit the gauzes of the queen and workers more often (Fig. 1, C/D).

Aggressiveness was shown towards the reintroduced maternal queen, but not to the familiar alien queen (Tab. 1, C/D). These results could suggest that both types of queen were attractive to workers, but that queen recognition was disrupted.

### 3) *Effect of transplantation on worker behaviour towards their maternal queens (A) and reintroduced maternal queens (C) (Tab. 1, A/C).*

At 2 months, the frequencies of behaviour in the two groups were similar, except that the frequency of immobility was significantly higher ( $P < 0.0001$ ) and that of self-grooming significantly lower ( $P < 0.01$ ) than in the alien-reared workers. Visits to the queen and worker gauzes were equally frequent in the two groups. A more detailed analysis of the behavioural repertoire confirms this picture (Fig. 1, A/C). Assuming that maternal queens are as attractive to workers that have been definitively reared with an alien queen as to those that were not, the degree of agonistic behaviour (observed in two of three tests) indicates that rearing with an alien queen disrupts worker behaviour towards the maternal queen.

### *Effect of transplantation on worker behaviour towards unfamiliar alien queens (B) and familiar alien queens (D) (Tab. 1, B/D).*

At two months, workers tested with a familiar alien queen were immobile less frequently ( $P < 0.001$ ), and showed other types of behaviour more frequently ( $X^2$  not significant) than their counterparts tested with the unfamiliar queen (Fig. 1, B/D). This increase in repertoire suggests that these workers learned the cues from the alien queen. Detailed analysis of the repertoire shows that workers tested against a familiar alien queen made more frequent visits to queen gauze, and also bit it very often. This analysis confirms that behaviour at or towards the gauze surrounding the queen is a measure of behavioural development in the young workers.

No agonistic behaviour towards the queens was recorded for group (D) workers at any age, again suggesting that familiarization involves learning the cues produced by the alien queen.

### *Effect of transplantation on worker behaviour towards maternal queens and familiar alien queens (Tab. 1, A/D).*

At 15 days after emergence, workers responding to a familiar alien queen (D) were stationary less often ( $P < 0.05$ ) and showed significantly more antennal



contacts, licking, trophallaxis ( $U = 0$ ,  $P = 0.05$ ) and self-grooming ( $U = 0$ ,  $P = 0.05$ ) than the other group (A). Their repertoire was more varied ( $U = 0$ ,  $P = 0.05$ ). At one month, these differences were no longer evident. At two months the behaviour of the two groups was indistinguishable in frequency. The repertoire of workers with the familiar alien queen was, however, significantly more diverse in worker compartment ( $U = 0$ ,  $P = 0.05$ ), (Fig. 1, A/D). In neither group of workers at any age was aggressive behaviour towards queens observed. This suggests that the familiar alien queen had been fully accepted by the workers.

*Effect of transplantation on worker behaviour towards unfamiliar alien queens (B) and reintroduced maternal queens (C) (Tab. 1, B/C).*

The maternal queen remained more attractive to workers than the unfamiliar alien queen, even though the workers had been separated for a time from their maternal queen. This is consistent with the results of Brian (1988). At two months, the frequency of locomotory activity did not differ significantly between the two groups, but group (C) workers made more visits to the queen gauzes ( $P < 0.0001$ ) (Tab. 1, B/C). As at one month, group (C) workers showed significantly less frequent visits to workers gauzes than group (B) workers ( $P < 0.001$ ). Group (C) workers also bit the queen gauze significantly more frequently ( $P < 0.01$ ), (Fig. 1, B/C).

Agonistic behaviour towards both queen types was recorded for 1 of 3 and 2 of 3 tests in one- and two-month-old workers respectively. Aggression to the reintroduced maternal queen suggests that familiarization with an alien queen disrupts queen recognition. On the other hand, attraction to the maternal queen is unaffected.

Results of experiments 1 and 2 show that the counts are highest in situations where the workers are familiar with the queen, whether maternal or alien. The additional stimuli could be odours equivalent to nestmate recognition cues. In the same way, workers attack those queens they do not recognize as nestmates.

## Discussion

Results of experiment 1 show that both familiar and unfamiliar queens are attractive. There is a difference between the two situations. Counts on queen gauze are far higher in the presence of the maternal queen. Vander Meer et al. (1980) demonstrated that queens produce a volatile worker attractant which is not queen specific. The *Solenopsis invicta* queen pheromone effectively attracted workers from any colony. Nevertheless, in this species, alien queens suffer aggression when introduced into a colony (Fletcher, 1987). In the monogynous species *Cataglyphis cursor* alien queens are attacked and killed. Aggression of alien queens has been described frequently (Wallis (1961) in *Formica fusca*; De Vroey and Pasteels (1978) in *Myrmica rubra*; Mabelis (1979) in *Formica polyctena*). If the colony is made queenless, however, workers will usually accept a mated

queen and rear her progeny. In *Myrmica rubra*, a polygynous species, workers have been observed to accept and aggregate around queens from neighbouring nests (Cammaerts and Cammaerts, 1984). Agonistic reactions are particularly severe between workers and queens from colonies more than a few kilometres apart. The frequency of aggressive behaviour by workers towards alien queens declines the longer the two are associated, and workers eventually aggregate close to the queens. When maternal queens are reintroduced to these workers they are rapidly recognized, and there is no difference in the degree of aggregation shown by workers responding to familiar alien or maternal queens. These results show that the ability of workers to discriminate between queens, and their tendency to be attracted to them, are connected. Both abilities depend on an intricate process of communication between queens and workers.

The results of experiment 2 show that workers continue to respond to attractant cues from their maternal queen after removal and exposure to alien odour queen.

A first hypothesis with the statement of a learning process could explain these responses. Most studies of cue learning deal with inter-individual recognition (see review by Jaisson, 1985). Two stages seem to be important: those before and those immediately after the emergence of the adult insect. Brian (1986) remarked that bonding is most easily established soon after emergence. Cues from the maternal queen could also be learnt by workers in the larval stage. Such preimaginal learning was described by Isingrini et al. (1985) in the context of brood recognition in *Cataglyphis cursor* workers, and in *Camponotus floridanus* by Carlin and Schwartz (1989). Our design in this study also involves that young workers are able to learn cues allowing recognition and attraction to the maternal queen in the 48 hours of adult life spent in the home colony before transfer to a new nest. Nevertheless, in order to demonstrate that attraction mediated by learning, it would be necessary to modify our experimental plan, for example with exposure first to one type of alien odour during larval life, second to another alien odour after metamorphosis, and then offer a choice between the two (Carlin and Schwartz, 1989).

The alternative hypothesis is that the maternal queen odour is similar to worker odour. Workers simply respond to odours similar to their own through the self-matching recognition process. The stimuli could be to some extent part colony odour, equivalent to nestmate recognition cues. Persistent recognition after the removal of the maternal queen is consistent with a chemical study of Nowbahari et al. (1990). These authors indicated a predominant endogenous component in *Cataglyphis cursor* colony odour.

In fact, it is of little importance how the persistent recognition of the mother queen originates, in comparison with its modification by post-imaginal experience.

Efficient response to attractant stimuli from queens develops in *Cataglyphis cursor* workers at 2 months after emergence. At this age, workers are sexually mature, and potentially capable of laying eggs in the absence of queen inhibition of oocyte development and egg laying. Behavioural expression of this response to queen recognition cues seems to be dependent on pheromones, and linked with the inhibition of ovary development. Fletcher, in a review paper (1987),

described the existence of two suites of recognition signals, one dealing with nestmate recognition and the other with the identification of social status. Keller and Passera (1989) thought that the relation between queen attractant cues and queen recognition cues may come about in two ways: either queens produce a single pheromonal complex acting both as a worker attractant and a queen recognition signal, or queens produce two different pheromones. Further identification and synthesis of these pheromones or pheromonal complex is required. A queen-specific chemical and its source has been identified in only one species, *Monomorium pharaonis*, by Edwards and Chambers (1984).

Young *Camponotus vagus* workers separated as pupae from older workers and kept separate for several days after adult emergence tend to be aggressive towards other colony members. This was never so when young workers were allowed to remain in the colony until a few hours after emergence as adults (Morel, 1983). Agonistic reactions by 15-day-old *Cataglyphis cursor* workers of groups C and D were prevented by the few hours they had spent in their maternal colony. Aggression was more frequently expressed as the workers aged, for example in group C. The aggression shown by group C workers to the reintroduced maternal queen suggests that workers are attracted to the maternal queen, but do not recognize her as nestmate. This dichotomy suggests that recognition of queens and attraction by them are independent processes.

Thus, young *C. cursor* workers can distinguish nestmate from non-nestmate queens. The differential in experiments 1 and 2, particularly the release of typical queen-orientated behaviour and the lack of agonistic behaviour towards alien queens confirms that workers were more attracted to an alien *C. cursor* queen to which they had been familiarized. The continual presence of the queen was necessary for queen attraction to be fully expressed (Berton et al., submitted).

Post-imaginal experience took place just after emergence, when young ants adsorb lipids that constitute the biosynthesized epicuticular layer (Blum, 1987; Franks et al., 1990) that is at least partly responsible for colony odour. It is therefore possible for young workers to adsorb alien cues at this stage. This explanation appears to be insufficient to explain our data. The characteristics of colony odour should not be greatly altered by transfer of workers to alien colonies, even for long periods (Nowbahari et al., 1990).

Experiments 1 and 2 clearly showed worker behavioural ontogeny. Changes in the population structure of small groups of worker ants or bees may induce changes in the pattern of behavioural development (Kolmes and Winston, 1988). Removal of older workers may accelerate the physiology, and thereby change the role, of younger workers (Lenoir, 1987). In the present study, the physiological development and associated behaviour (movement, ability to recognize cues specific to queen, and number of behaviour types in the repertoire) developed similarly in workers reared with an alien queen (groups C and D) and those reared with their maternal queen (A and B).

Tests of queenless young *C. cursor* workers against their maternal queen or a familiar alien queen produced a shift in development and behaviour, for example in locomotion, through delayed physiological maturation (Berton, 1989). Among queenless workers, the ages at which various types of behaviour are ex-

pressed are different from those seen in workers with queens. On these grounds, it is likely that the response of workers to queen attractant cues would be greatly modified by lack of queens. Our behavioural data (op. cit.) indicate that workers at 4 months after emergence display the unique, strikingly marked, queen-induced response, accompanied by strong agonistic reactions. Queen recognition and attraction by the queen are still separate at this age.

Through their power of attraction, maternal or familiar alien queens promote harmonious development of individual ants and of the colony. Attraction of workers to the queen fosters contacts allowing discrimination between individuals, and promotes integration within the colony.

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