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AGE-RELATED CHANGES IN AGGRESSION IN ANT CATAGLYPHIS CURSOR (HYMENOPTERA, FORMICIDAE): INFLUENCE ON INTERCOLONIAL RELATIONSHIPS

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ABSTRACT: Age-related changes in aggression in ant Cataglyphis cursor (Hymenoptera, Formicidae): influence on intercolonial relatioships.
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Cataglyphis cursor forms monogynous societies which may however accept some foreign individuals. The factors influencing the degree of aggressiveness of the workers have been studied as follows. We have shown that the aggressive behaviour is expressed mainly by the foragers, the nurses are very little aggressive. We observe therefore an evolution in the reactivity of the workers to a foreign odour in terms of age-related changes. However the closing of the society still depends on the behaviour of the foragers.

Among the social insects young workers are generally adopted by foreign colonies even if these colonies are completely closed to any other adult ants. Experiments allowed us to specify that young workers are recognized as foreigners by another colony after the 4th day of age. Afterwards the adopted young ants were put back at different ages into their original colony, where they were recognized and accepted by their sisters.

The discussion is based on the origin of the colony odour. If this odour is formed from cuticular substances, in C. cursor their origin is probably endogenous, and predominant in comparison with the odours acquired from the environment (including that of the adoptive colony). Such an individualistic recognition system is known in only one other social insect species, the sweat bee.

Key words: Hymenoptera, Formicidae, Cataglyphis, Aggression, Age polyethism, Colony odour, Recognition

INTRODUCTION

It is well known that many social insects are able to discriminate nestmates from other conspecific individuals ; as a consequence, strongly antagonistic reactions towards non-nestmates appear. This will affect patterns of interference competition and nest distribution (Fielde, 1903 ; Wilson, 1971 ; Hölldobler and Michener, 1980 ; Mintzer, 1982 ; Jaffé and Marcuse, 1983).

Although the monogynous ant species principally make very closed colonies (Hölldobler and Wilson, 1977), Cataglyphis cursor appears to be an exception to this rule. This mediterranean ant forms monogynous societies which may however accept some foreign individuals (Nowbahari and Lenoir, 1984). In previous works we have shown that a correlation may exist between the closed state of the colonies, which is indicated by degree of aggressiveness towards strangers, and the geographical distance of origin of the stranger.

In fact, the introduction of adult intruders into a colony have shown some cases of adoption ; it means that within the same habitat 54% of ants are adopted but, there is no possibility of adoption in the case of very distant regions, like Pyrénées - Orientales (Banyuls) and Vaucluse (Apt), which are separated by the Rhône. In the latter case, in more than 190 tests the adult intruders belonging to distant colonies have always been vigourously attacked and killed by resident foragers (Nowbahari and Lenoir, 1984).

In the present study we attempted to analyse :

1) whether the aggressive reactions or, more exactly the discrimination of foreigners, is a forager or a nurse role in relation with polyethism or division of labour.
2) on the other hand our purpose was to observe whether the social environment in which the animal is reared could be as important as the endogenous odours.

MATERIAL AND METHODS

Laboratory conditions

The different colonies were maintained in the laboratory in artificial nests under controlled homogenous conditions to reduce as much as possible the influence of nutrition and temperature on behaviour. Medium size colonies were chosen, containing generally 500 individuals and a queen.

The nest room was maintained wet and was connected to the foraging area (30 x 30 cm) with a tube. The temperature was 24° - 26°C. These physical parameters were similar to those recorded in the field during the hours of high activity. Food consisted of mealworm larvae and honey distributed twice a week to all the colonies.

Experiment I

In insect societies the influence of age on polyethism or division of labour is well known. Amongst ants the young workers usually serve inside the nest first and busy themselves outside the nest only later ; the foragers defend the colony in addition to their predatory and gathering roles (Wilson, 1971).

Experiment I was conducted to test this phenomenon. As these animals are eusocial insects, it seemed appropriate to consider a possible group effect on behaviour. Consequently, two groups of five ants from distant colonies in which inter-colonial adoptions are impossible, for exemple (Banyuls and Apt) (Nowbahari and Lenoir 1984) were placed together in round boxes (Diameter 6 cm). The ants belonged either to the same or to different behavioural caste (forager, or nurse). Each test was replicated 4 times. The aggression behaviour was observed during 30 minutes. After a delay of three days we noticed the percentage of mortality.

In these experiments the foragers were distinguished by their gathering role in the exterior area and the nurses by their larvae carrying role in the nest chamber.

Experiment II

The factors influencing the degree of worker aggressiveness have been studied in a laboratory situation. We have conducted experiments which enable us to determine the age at which workers are recognized as foreigners by another colony ; also we have tried to find whether there was any change with age in the reactivity of the workers with regard to a foreign odour. Many authors now consider that the colony odour in social insects originates from cuticular substances (Howse 1975, see review by Howard and Blomquist, 1982).

Experiment II A was done with the introduction of freshly hatched 0 to 8 hours old and young ants of different ages : one, two, three, four days and more than four days old. The ants were introduced in the exterior area of a foreign colony. We have tested the young ants of eight distant colonies (Banyuls/Apt) in which the control adults have never been accepted. Generally the newly-hatched ants were marked with a dot of paint and they stayed in their colony until the transfer into the foreign colony. In this way we have tested more than 350 newly-hatched ants. We have studied the resident ant behaviour towards the young intruders during 10 minutes after the introduction and after 24 hours. As the young ants are very fragile and die quickly after aggressions, the test is very selective.

Experiment II B was conducted in the same conditions with newly hatched ants introduced directly into the nest chamber of the alien colony.

In Experiment II C the same workers adopted during Experiments II A and II B were reintroduced into their original colony.

In experiments II an ant was considered as accepted when she could be observed into the nest chamber participating to the colony activities.

For the analysis of results the χ^2 test was used, calculated on the real data. In all the experiments the contribution of the two studied populations (Banyuls and Apt) were in equilibrium. As there was no difference in the results, the data are presented independantly of the origin of the workers.

RESULTS

Experiment I (fig. 1)

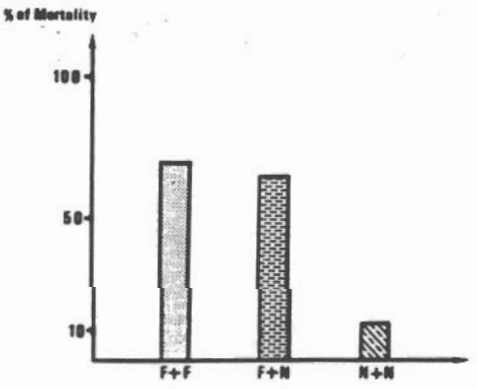

Fig. 1 : Aggression behaviour of the two different castes : Foragers F and nurses N - For each of the 3 situations 40 workers were used.
$\chi^2 = 32.476$ $p < .01$, 2 d.f.

The results of experiment I show that the foragers exhibit aggressive behaviours. When two groups of foragers are confronted, the mortality percentage varies from 60% to 80% (70% on average). When a group of nurses is put with a group of foragers there are also many aggressions and the mortality percentage is high, indistinctly for foragers or nurses, (65% on average). Finally in the case of two groups of nurses the aggressive behaviour is low : from 0% to 21%, (12.50% on average). The difference is not significant between the two groups including foragers (χ^2 = .057 NS, 1 d.f.). It is significant between these two groups and groups of nurses (χ^2 = 30.112, $p < .01$, 1 d.f.).

We can conclude that the age polyethism influences not only the task distribution but also the interactions between colonies. The result that foragers rather than nurses react aggressively to aliens is not particularly surprising, as this is the rule in all social insect species studied. This does not necessarily mean that foragers have higher discrimination capacities. They could simply be more aggressive. Nurses are younger, more fragile, and less expendable to the colony than foragers that will not live long anyway. Thus nurses are expected to be less aggressive; they could discriminate aliens just as well as foragers can, but avoid them in experimental encounters rather than attacking.

This discrimination towards the intruders plays an important role in the "close-state" of the societies and therefore in their competition and distribution.

Experiment II A (fig. 2)

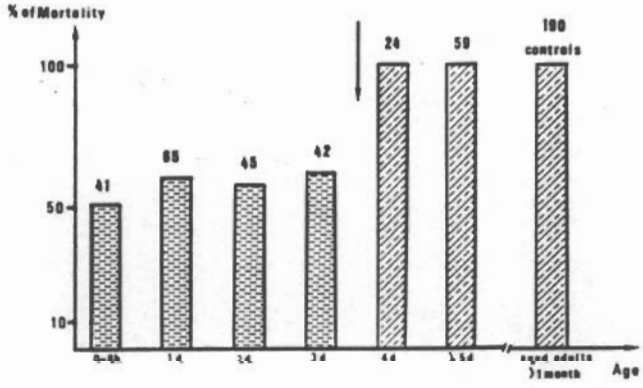

Fig. 2 : Progressive rate of aggressiveness in relation with the age (hours : h ; day(s) : d
For each age the number of tested ants is reported on the graph.
χ^2 = 132, ($p < .01$, 6 d.f.), χ^2 for less than 4 days = 0.156 (NS - 3 d.f.)

The results of the second part of the experiments show that contrary to the older adults, the newly-hatched adults are frequently but not invariabily adopted in a foreign colony, 40% on average. It means that C. cursor foragers even distinguish many of these young intruders but not all. This discrimination increases sharply as the ants become older. The foragers perfectly distinguish all the foreigners and vigourously attack them when they are 4 days old or more as indicated by the arrow on Fig. 2. Thus the first four days of life may represent an important period for the establishment of the individual's odour. In control experiments newly hatched ants were deposited into the foraging area of their own colony, they were always very quickly received to the nest without any hostility.

Experiment II B

As we saw that the aggressive behaviour of foragers and of nurses is different, we introduced the newly-hatched workers directly into the nest room of the foreign colonies (37 young workers were tested). Under this condition we observed a higher rate of adoption with less aggressive behaviour : where nurses were the principal type of resident ants 86% of ants were adopted ; it means that out of 37 introductions, 32 young workers were adopted and only 5 were killed.
These results must be compared to the results of experiment II A where 50% of introduced newly-hatched callows are killed by the foragers (χ^2 between II A 0-8h and II B = 10.804, $p < .01$, 1 d.f.).

Experiment II C : Table 1

38 young workers adopted by foreign societies during experiments II A and II B were later reintroduced into their original colony, after various delays (from two days to eleven months, the young workers being then at least darkly pigmented). After a short period of slight initial aggression, the reintroduced ants were identified as nestmates by resident ants and rapidly transported into the nest. 100% were adopted (Table 1). It was verified that adopted workers were not numerous in the foreign colony so that adopted workers did not have effected its colony odour. They were observed into the nest amongst alien ants. So these workers, which have spent a part of the first four days after hatching in a foreign colony, are recognized by members of two colonies: their own nestmates and the adoptive colony residents.

In control tests we verified that the mortality of young ants was not due to their fragility. The transportation by foreigners could hurt them. So we tested 34 freshly-hatched ants which were placed in the external area of their homocolonial colony. We noticed that, even if the transportation of a congener is always preceded by a very short "aggressive like phase" in which an ant grasps a worker and pulls it

towards itself, the young ant is never killed by its homocolonial nestmate. This "aggressive phase" probably has nothing to do with aggression. It may be ordinary recruitement for social carrying, as reported in many ant species.

Age of ants	Number of ants	% readoptions
2 days	5	100 %
3 days	17	100 %
4 days	1	100 %
5 days	2	100 %
6 days	1	100 %
10 days	2	100 %
11 months	10	100 %
Total	38	100 %

Table 1 : Readoption of ants various age into their origin colony. The age represents the duration of study in the adoptive colony.

CONCLUSION AND DISCUSSION

The results clearly indicate the high capacity of discrimination of non-nestmates, even the very young strangers specially by foragers. These results are in contradiction not only with previous works in other species which suggest that newly hatched ants are always adopted in foreign colonies of the same species (Forel, 1874) but also of other species (Forel, 1874 ; Fielde, 1903 ; Delage and Jaisson, 1969 ; Jaisson, 1972, 1980 ; Le Moli and Mori, 1984 , 1985 ; Carlin and Hölldobler, 1983 ; Errard, 1984). Generally the young ants of the two species were put together in small groups, which could enhance the interindividual tolerance. In C. cursor, the callow introduced into the nest of an alien society was always adopted (Lenoir et al. 1982). The substantial difference with the results presented here (86% in experiment II B) could be explained by the choice of the colonies : in 1982 the colonies came from neighbouring places, and adoptions of mature adults were easier as shown by Nowbahari and Lenoir (1984) . In this experiment we chose completely closed colonies where mature adults are never tolerated and 40% of young workers were adopted. This discrimination capacity appears to be more developed in foragers. Bonavita and Morel (1984) found the same result in Camponotus vagus and it is well known in ants that foragers generally show more responsiveness in the defense reactions of the colony (Dobrzańska 1959 ; Weir, 1958 ; Cammaerts-Tricot, 1975 ; Lenoir and Ataya, 1983). In fire ants Solenopsis invicta, unfamiliar queens introduced into a colony are executed predominantly by foragers, which confirms that the sensitivity of workers to queen pheromones and colony odour changes as a worker ages (Sorensen and Fletcher

1985).

Cuticular hydrocarbonsare at least partly responsible of colony odour in social insects and lure experiments demonstratedit in Cataglyphis cursor (Lenoir and al., 1988). The origin of the hydrocarbons is not known.

Experiment II A indicate that the distinctive odour of Cataglyphis ants seems to be predominantly endogenous. Also, the remarkably immediate acceptance of nest-mates previously adopted in a foreign colony and re-introduced into the original colony after different delays (cf experiment II C) shows that the endogenous characteristics are an essential and stable factor in this individual odour formation. This experiment, plus the result that a large proportion of workers are already unacceptable in alien colonies on the day they eclose, suggests that endogenous cues are the principal source of colony odour and that individuals that coexist with aliens even for prolonged periods do not acquire odours from them. Such an individualistic recognition system is known in only one other social insect species, the sweat bee Lasioglossum zephyrum (Greenberg, 1979). Other experiments demonstrate that the social environment can be essential to the ontogenesis of the interindividual recognition processes. Examples can be found in the discrimination of cocoons (Jaisson, 1975 ; Le Moli and Passetti, 1977, 1978) and larvae (Lenoir et al., 1982 ; Lenoir, 1984 ; Isingrini et al. 1985).

We have shown that progressive changes with age in the odour of individuals may be important and that significant changes occur in the individual odour during the first four days of C. cursor life. It may represent a sensitive period for the establishment of the individual's odour. It is remarkable to notice that the first days posthatching represent a very important period for the individual life. This sensitive period has been already identified by several authors to distinguish between con and allospecific cocoons (Jaisson and Fresneau, 1978 ; Le Moli and Passetti, 1977, 1978), the development of nursing behaviours in Ponerine ants (Champalbert, 1986) and bonding between workers and queens in Myrmica (Brian, 1986).

It is not known if workers less than 4 days old are already carrying the odour of their nest of origin. This period could be important for physiological maturation and the individual is particularly opened to the informations coming from the environment. We could imagine a process of progressive appearance of the odour during this period. More experiments are necessary to know the chemical substances responsible of the colony odour and to test the existence of a sensitive period for its establishment.

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