Influence of preimaginal experience on the social behaviour of adult ants and the importance of fellowship in nestmate recognition

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I INTRODUCTION

The closure of social groups is frequently seen in Primates and many other Vertebrates. It is almost the universal rule amongst the insect societies where it is highly correlated with colonial recognition. Numerous recent studies have been devoted to this problem in social Hymenoptera, which explain how the individual can be integrated into the society. This inter-individual recognition is based exclusively upon chemical signals. This is demontrated by either the rejection of individuals recognized as intruders, or by positive responses to those accepted into the society (see reviews by Wilson 1971, Jaisson 1985, Isingrini and Lenoir 1986).

Recent data have shown that colonial identity is based upon cuticular substances, the origin of which (endogenous or environmental) is not wellknown. Porter (this volume) employed the term phenotypic signature proposed by Holmes and Sherman (1982) to define this chemical complex. The members of the society are identified by these substances. Breed (this volume) supposed that each individual has integrated, during its ontogenesis, the information given by colonial signals, finally achieving an internal recognition template (that is a standard of comparison - see Holmes and Sherman, 1983).

The development of this recognition template has also been studied during the last few years. It has two major interests. First, it gives information about the process of integration of the individual into the society. Secondly, in the context of the kinship theory (Hamilton - Wilson sociobiological model), there is an implied relationship between altruistic behaviour and kin recognition, because in natural conditions each colony is a family group. The concept of inclusive fitness, fundamental in the kinship theory, implies the existence of mechanisms allowing recognition of relatives, indispensable if altruism is a positive genetic investment. This lead one to experimentally investigate the correlation between social behaviour and genetic relatedness.

In this context, Greenberg (1979) has achieved hybridizations of Lasioglossum zephyrum, providing 14 degrees of genetic relatedness. On the basis of acceptance or rejection experiments he was able to show a positive correlation between acceptance of the intruder presented at the nest entrance and relatedness between intruders and guard bees. This work is a precise analysis of the capacities of social insects to recognize the degree of kinship, and thus for orientating their altruistic behaviour.

From a general point of view, the discrimination between homocolonial and alien individuals, demonstrated in many social Hymenoptera (see review by Isingrini et al. 1985), supports the kinship theory because of the genetic relatedness between individuals belonging to the same colony.

The individual and society, Ed. by Luc Passera & Jean-Paul Lachaud, Privat, I.E.C., Toulouse, 1986, pp. 49-53.

2 DEVELOPMENT OF COLONIAL RECOGNITION

According to Breed (this volume) there are two basic ways in which a social insect might gain the information necessary to discriminate nestmates from non-nestmates. First, they might have a genetically programed recognition template permanently compared with the phenotype of each individual encountered. Secondly, the insect might learn its own characteristics or those of surrounding individuals.

In the case of social insects, a genetic origin for the recognition template can no longer be reasonably defended. On the contrary various data have shown the importance of the early social environment during ethogenesis (see above mentioned reviews).

In this paper data concerning colonial recognition of larvae by adults are reported. In Cataglyphis cursor, Lenoir (1984) has demonstrated that callow ants prefer to tend larvae belonging to their own nest, even immediately after emergence. Isingrini et al. (1985) have recently shown that this apparently spontaneous preference is due in fact to an early learning process achieved during the larval stage.

In a first set of experiments, the possibility of learning during the first ten days of imaginal life was investigated. With adoptions or complete isolation of the individuals, it was shown that the colony-brood recognition can become established during this period. Nevertheless this acquisition is not sufficient to allow an inversion of the natural preference for nestmate larvae. In other words the preference for the sister brood was merely attenuated, but not reversed, by their post-hatching experience. These results are at least consistent with the hypothesis that colony- brood recognition could be learned during preimaginal life.

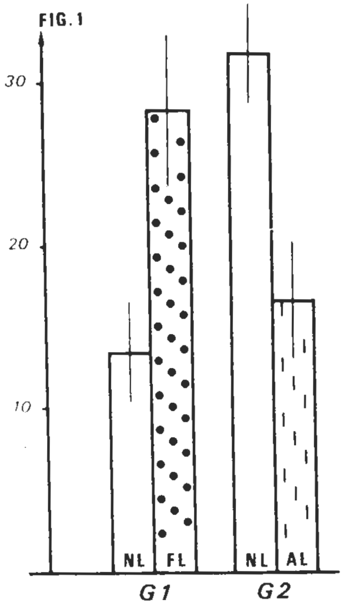
As a consequence the hypothesis of a preimaginal learning was investigated in a second set of two experiments.

First - Cataglyphis cursor eggs were transferred from their parent colony into one of three recipient colonies. The larvae produced from these eggs spent their whole larval stage in the alien colony.

Soon after pupation, the cocoons of the experimental larvae were transferred back into their parent colony, where they spent on average 15 days before eclosing. The workers that emerged were tested at age five days by being given a choice among three of their own nestmate larvae (NL) and three larvae from the familiar colony (FL). For this test, the callow ants were placed in 12 groups of two to five each, with the six larvae, and were tested for 30 min (the total number of ants was 48). Figure 1 clearly shows that the ants preferred the larvae of the familiar (alien host) colony, FL ($P < 0.01$). Control ants prefer nestmate larvae to alien unknown larvae ($P < 0.01$) These results demonstrate that learning took place during the larval stage.

Second - To confirm this observation, larvae of different stages of development were transferred to adoptive colonies.

The small and large larvae of two colonies were separated. For each brood, these small or large larvae were transferred as a group into a recipient colony (the "familiar colony") whose own brood had been eliminated. The large larvae spent from two to five days in the familiar colony before pupation, and the small larvae, from 10 to 20 days ; as a consequence, the larval size was inversely related to the duration of the preimaginal experience in the familiar colony. A total of 105 workers emerged from the group of large larvae (group G1) and 77 from the group of small larvae (G2). These adopted individuals were reared in the familiar colony until three to seven days after their emergence into adult life. Within each group, the newly emerged workers were then divided into subgroups of seven individuals. Each of these subgroups was given three choice-tests, lasting ten min each, the choice being between four NL and four FL. As Figure 2 shows, the workers that had been transferred as large larvae (G1) preferred their NL ($P < 0.01$), whereas workers that had been transferred as small larvae (G2) preferred the FL ($P < 0.01$). So adult ants that had spent most of their larval life in an alien colony preferred nursing the larvae of that colony to nursing their own sister larvae.



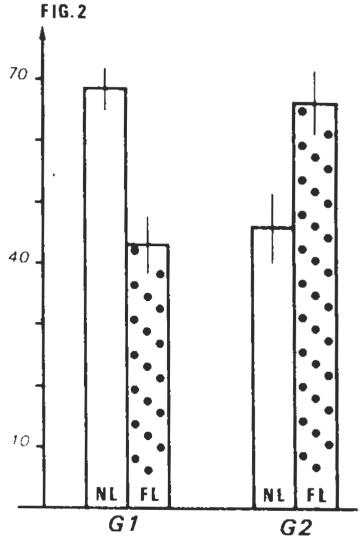


Fig. 1 and 2 : Mean numbers (and confidence intervals) per adult ant of instances of brood-nursing behaviours directed towards larvae in choice situations (from Isingrini et al., 1985).

NL : Nestmate Larvae
FL : Familiar Larvae
AL : Alien Larvae.
Fig. 1 - G1 : ants having spent their whole life in the recipient colony (egg transfer) -G2 : control ants.
Fig. 2 : ants transferred to the recipient colony as large larvae (G1) or small larvae (G2)

The results of this experiment show that colony-brood recognition, as reflected in the nursing behaviour of workers, cannot be altered during the last instar of larval life. This might be attributable either to the existence of a more sensitive period in the first instars for larval development or the total duration of the exposure to the colony odor.

3 DISCUSSION

3.1 Individual imprinting and social cohesion

In the ant Cataglyphis cursor, a certain familiarization during the first days after hatching can affect colony-brood recognition. This phenomenon confirms the existence of a high capacity for learning during this period as suggested by previous, independent studies (see review by Isingrini et al. 1985, and more recently Le Moli and Mori 1984, 1985).

However, the main process affecting colony-brood recognition seems to occur during the larval life. Information acquired during this stage persists through metamorphosis into adulthood. Preimaginal learning has previously been reported only for feeding behaviour in solitary insects.

The main experiments on this topic have been presented by Thorpe and Jones (1937) who showed that adult females of Nemeritis canescens lay preferentially on the host on which they lived during larval life. Borell du Vernay (1942), then Alloway (1972) trained Tenebrio larvae in a T maze with alimentary rewards. They observed that the adults obtained in these conditions learned the maze more quickly than inexperienced controls. Cushing (1941) and Manning (1967) obtained Drosophila adults familiarized to a repulsive odour by rearing the larvae with a diet containing this odour. More recently Marenco et al. (1984) modified the learning capacities of adult Drosophila by manipulations of the larval diet. Nevertheless it seems that a preimaginal learning is demonstrated for the first time in the ethogenesis of insect social behaviour. It appears that the concept of imprinting could explain the learning process involved in colonial recognition of Cataglyphis cursor.

Indeed the classical characteristics of imprinting can be found : occurring early in the life, very difficult to be reversed and establishing a strong delayed link between the individual and the imprinted object.

Imprinting with a colonial odour is an ontogenetic process, which allows efficient and persistent segregation between societies. A flexible adaptation to the high variability of the colonial stimulus and to its modification during the evolution of the species is possible. The variations could be produced either by genetic drift in the case of an endogenous determinism of odours, or by modifications of the habitat in the case of an environmental determinism. Considering that imprinting is just as steady as a genetic determinism, the social cohesion can be maintained permanently.

3.2 Fellowship and kin recognition

This research suggests the merit of studying the mechanisms of kin recognition, which is fundamental to the sociobiology of altruism.

The departure point of the ethogenetic process is the fact that the individual is born within the nest. This results in spacial restriction that constrains this individual to live within a group genetically related to him. One finds many varieties of early learning processes that occur either in the neonatal period for vertebrates or in the immediately post-emerging or even larval stage for the social Hymenoptera. These processes result in the development of fellowship status between individuals which is crucial for kin recognition.

The discovery that larval learning affects colony-brood recognition by adults, as demonstrated in Cataglyphis cursor, suggests how the correlation between altruistic behaviour and genetic relatedness, which is explained by kinship theory, might be established.

Fellowship between larvae and heterocolonial workers results in the establishement of "kin" recognition directed towards the adoptive parents. The young workers subsequently display preferential nursing towards the larvae of the adoptive colony at the expense of their genetic sisters. This very early familiarity thus is resistent to metamorphosis, and guarantees that under natural conditions recognition will be associated with a de facto correlation between genetic relatedness and social behaviour, because of the superposition between fellowship and kinship.

The concept of fellowship therefore seems to better account for the orientation of altruistic behaviour, whose evolutionary significance is revealed by the concept of kinship. In non-parasitic species, the workers and the larvae of a colony are genetically related to each other. Thus, the ethogenesis of the individual during its larval stage will normally direct the altruistic behaviour towards the kin, and this recognition will be reinforced by the worker's experience following its emergence.

The reality of the biological cycle results in the fact that the cues of familiarity recognition and genetic-relatedness recognition are usually superimposed. The very existence of fellowship is the means by which social integration becomes a favourable compromise between the guarantee of the genetic investment of solitary strategies and the inclusive fitness of social strategies.

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