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## EVOLUTION OF EUSOCIALITY : LESSONS FORM THE MECHANISM OF NESTMATE DISCRIMINATION IN THE PRIMITIVELY EUSOCIAL WASP *ROPALIDIA MARGINATA*

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The multiple origins of eusociality in the Hymenoptera have been ascribed to the genetic asymmetry created by haplodiploidy such that full-sisters are more closely related to each other than a mother is to her daughters (1). However, many Hymenopteran queens are known to mate multiply and simultaneously use sperm from different males and thus produce different patrilineages of daughters. This destroys the asymmetry created by haplodiploidy unless full- and half-sisters can be discriminated and preferential aid given to the former (2).

Female wasps of the primitively eusocial wasp *Ropalidia marginata* (Lep.) (Hymenoptera : Vespidae) can discriminate nestmates from non-nestmates outside the context of their nest. In order to do so however, it is essential that both the discriminating animals and the discriminated animals have been exposed to a fragment of their nests and a subset of their nestmates. This suggests that both labels and templates used in recognition are acquired by the wasps from such common sources outside their bodies as the nest or their nestmates. It appears unlikely therefore that full- and half-sisters or other genetic differences within a colony will be recognised. One implication of these results is that kin recognition is unlikely to restore the genetic asymmetries created by haplodiploidy but broken down by multiple mating (3) and serial polygyny (4) in this species. Eusociality is thus unlikely to be selected for by haplodiploidy alone in *R. marginata* (5). In general, we suggest that the multiple origins of eusociality in the Hymenoptera should be ascribed to haplodiploidy with caution (6).

A second consequence of our results is that acceptance and tolerance of conspecifics are likely to depend not merely on genetic relatedness but on other factors too. Here we describe results of experiments designed to explore this possibility. Pairs of nests were collected from localities separated from each other by at least 10 km to ensure that wasps eclosing from the same nest would be more closely related to each other than they would be to the wasps eclosing from the other nests in the pair. One nest was cut into three parts. One part was fixed in a cage and allowed to be regenerated by the adults present at the time of collection. All animals eclosing on the second fragment of the nest were allowed to remain on that fragment for a period of 10-20 days and were thus exposed to a fragment of their nests and a subset of

their nestmates. These constituted 'Exposed' relatives of the animals on the regenerated nests. From the third fragment animals were removed from their pupal cases prior to their natural eclosion and were thus not exposed to their natal nests and nestmates. These constituted 'Isolated' relatives of the animals in the regenerated nest. The second nest in each pair was cut into two halves, which were used to obtain 'Exposed' non-relatives and 'Isolated' non-relatives of the animals on the regenerated nest. Four wasps (which were at least one month old) of each of the four categories namely 'Exposed' relatives, 'Isolated' relatives, 'Exposed' non-relatives and 'Isolated' non-relatives were released into the cage containing the regenerated nest. Behavioural interactions between the nest animals and the introduced animals were recorded for three weeks after introduction.

In the three repetitions of such an experiment, a total of 46 animals were released. However, no animal irrespective of category, was accepted onto the colonies. But by means of tolerance indices used for quantifying tolerance of the nest animals towards the foreign animals, we found that, in the vicinity of the nest, nest animals were significantly more tolerant towards 'Exposed' relatives than 'Exposed' non-relatives. Away from the nest however, no category of introduced animals was treated more tolerantly than any other category by the nest animals. In fact, as if in accordance with the latter result, a satellite nest initiated by four foreign animals was joined by three nest animals. These findings seem to indicate that complex context-dependent rules govern tolerance and acceptance of foreign animals and that genetically unrelated individuals can sometimes cooperatively found nests.

Because genetic asymmetries created by haplodiploidy are unlikely to be sufficient to explain the presence of worker behaviour in *R.marginata*, we have begun to explore models of mutualistic interactions that might facilitate social evolution (5). The observations that factors other than genetic relatedness modulate acceptance of and tolerance towards foreign animals and that genetically unrelated individuals can cooperatively found new nests are clearly conducive to the development of mutualistic interactions that may facilitate the evolution of eusociality (7)

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