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The Evolution of Altruism in Insects – A Case Study

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INTRODUCTION

Termites, ants and some species of bees and wasps live in social groups of varying degrees of organization where individuals often cannot survive if removed from the group. Colonies of these social insects consist of one or a small number of reproductive individuals and a number of sterile workers. The sterile workers in social insect colonies spend their whole lives working for the well-being of their colony-mates and die without leaving behind any of their own progeny (Wilson, 1971; Michener, 1974; Hölldobler and Wilson, 1990; Ross and Matthews, 1991). How can the theory of natural selection, which is based on the concept of survival of the fittest, give rise to such altruism on the part of workers ? This question has bothered evolutionary biologists starting from the time of Darwin (1859, p. 236) who termed it "...one special difficulty, which at first appeared to me to be insuperable, and actually fatal to my whole theory." In the last 25 years there has been a great flurry of activity, both theoretical and empirical, bearing on this question. In what follows, I shall briefly describe the major theories that have been proposed and show how we have attempted to test these theories using the model system of *Ropalidia marginata*, a primitively eusocial tropical paper wasp.

PRIMITIVELY EUSOCIAL INSECTS

Many species of social insects, termed *highly eusocial*, have evolved to such an extent that their fertile and sterile members are morphologically differentiated. Some species of bees and wasps however, are said to be *primitively eusocial* because all members of the colony are morphologically similar and their fate appears to be quite flexible even in the adult stage. Such primitively eusocial species are ideal model systems for studying the origin and evolution of social life in insects. *Ropalidia marginata* and *Ropalidia cyathiformis* are two species of primitively eusocial paper wasps that are abundantly distributed in peninsular India (Gadagkar, 1991a). In these species new nests are founded throughout the year by one or a group of females (Fig.1). Female wasps produced on these nests have several options open to them. They may either leave to found new nests of their own, stay back and become workers or stay back and eventually become queens in their nests of birth (Fig. 2).

SOCIAL ORGANIZATION AND DIVISION OF LABOUR

By studying the behaviour of individually marked members of several colonies of *Ropalidia marginata* and *R. cyathiformis* we have discovered a large amount of inter-individual variability in behaviour. By multivariate statisitical analysis of this variation, we have been able to classify the members of a colony into three behavioural castes which we have called *Sitters*, *Fighters* and *Foragers* (Fig.3) (Gadagkar and Joshi, 1983; 1984). Of these, Foragers do bulk of the extra-nidal tasks of food gathering and have the most poorly developed ovaries. Sitters and Fighters have relatively better developed ovaries and share the intra-nidal tasks of building the nest and caring for the brood (Fig. 4). The Sitters and Fighters are different however, in that they appear to adopt different strategies of maximizing their chances of becoming reproductives. The Sitters seem to conserve energy by spending a large proportion

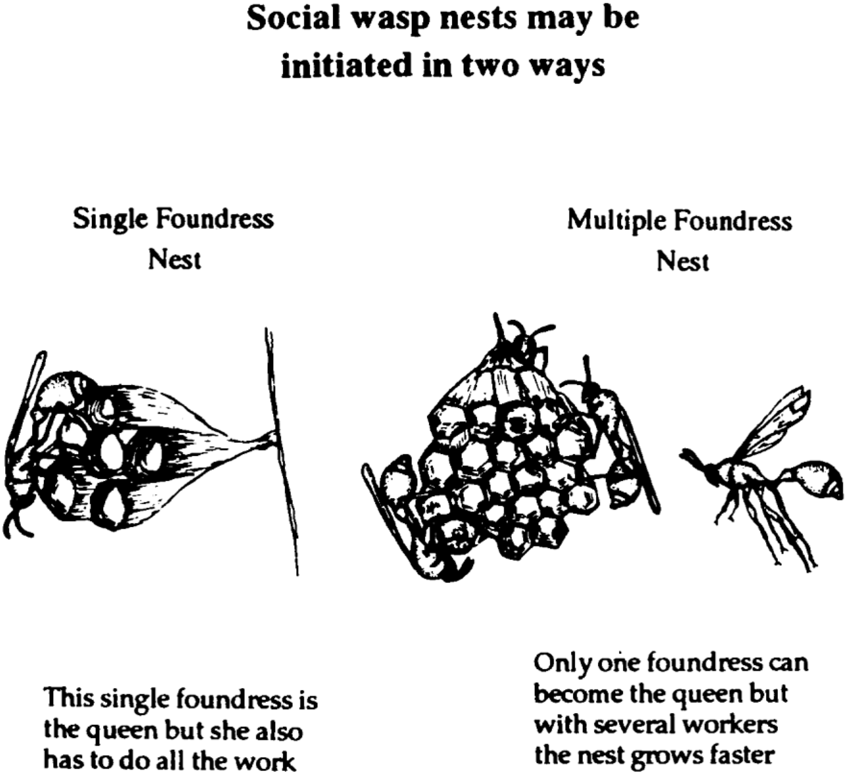

Figure 1. Modes of nest initiation in primitively eusocial wasps.

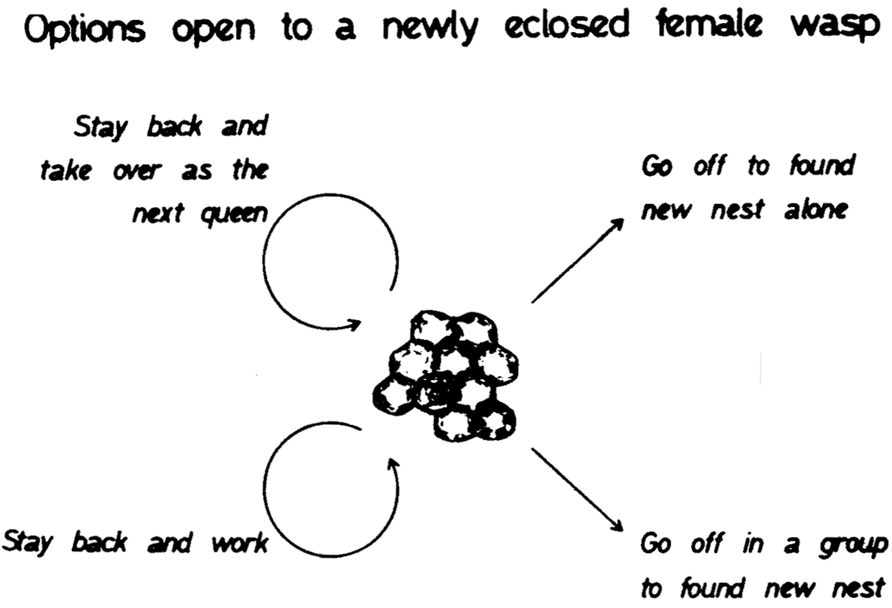

Figure 2. Reproductive options available to primitively eusocial wasps.

of their time in resting while the Fighters attempt to get at the top of the dominance hierarchy by indulging in frequent fights with their nestmates (Chandrashekara and Gadagkar, 1991)

GENETICS OF SOCIAL EVOLUTION

The first serious attempt to solve the puzzle of the apparently altruistic behaviour of the sterile workers in social insect colonies was made by Hamilton (1964a,b). He proposed a modification of the theory of natural selection which is often known as the theory of *Kin Selection* or *Inclusive Fitness Theory*. While producing offspring is one way of obtaining fitness, aiding genetic relatives is another, according to this theory. Hamilton's theory seems particularly applicable to the evolution of sterile worker castes in the Hymenoptera (ants, bees and wasps but not termites) because of their peculiar system of inheritance known as *haplodiploidy*. Males

Behavioural castes in a social wasp

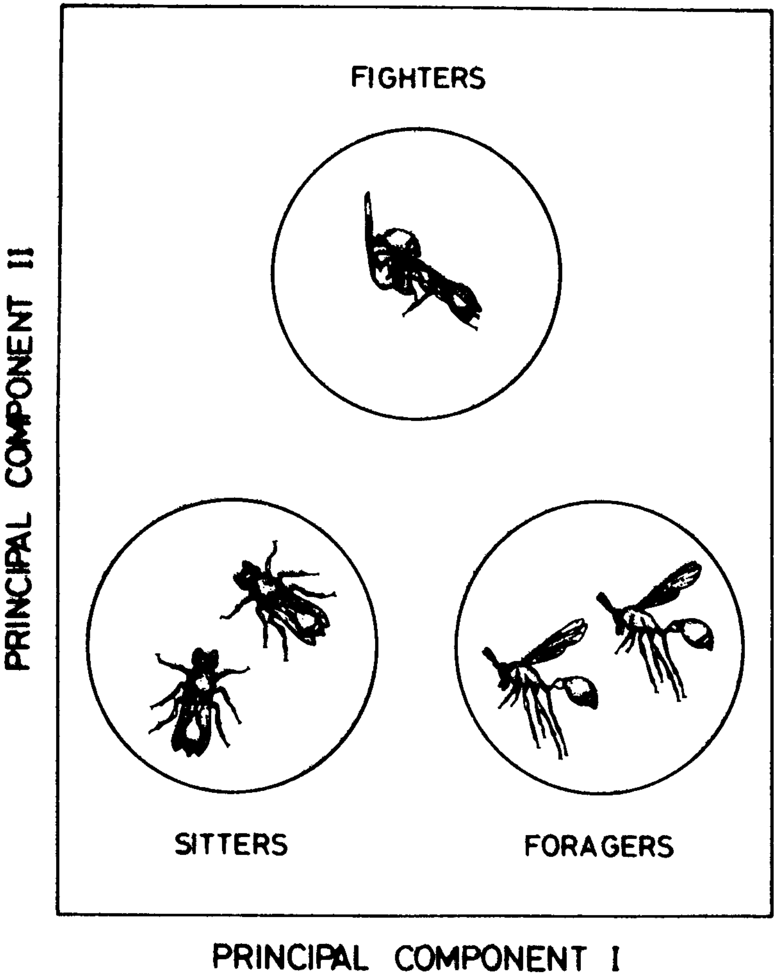

Figure 3. Behavioural castes in a colony of social wasps.

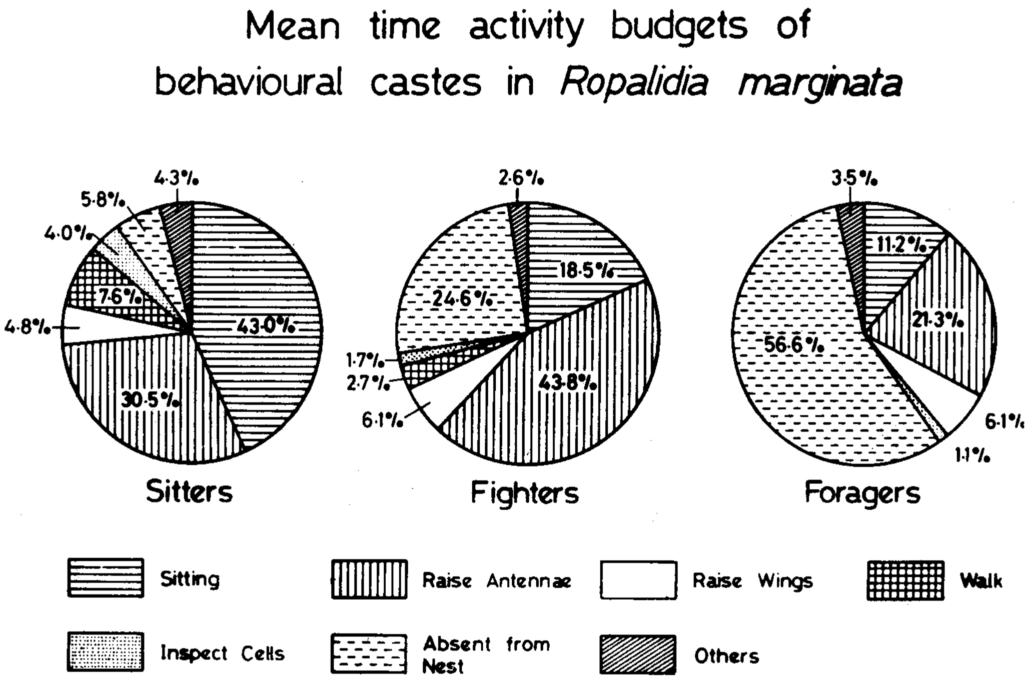

Figure 4. The manner in which the behavioural castes, sitters, fighters and foragers in *Ropalidia marginata* allocate their time between different activities.

develop from unfertilised eggs and are thus haploid while females develop from fertilised eggs and are thus diploid. This creates an asymmetry in genetic relatedness such that full-sisters are more closely related to each other than a female is to her offspring.

Our researches indicate however that this genetic asymmetry is broken down in *R. marginata* by two phenomena. First, queens are *Polyandrous*; they mate with more than one male, store sperm from each of their mates in their spermathecae and simultaneously produce different patrilines of daughters. In other words, not all daughters of a queen are full-sisters; colonies consist of a mixture of full-sisters and half-sisters (Muralidharan *et al.*, 1986; Gadagkar, 1990a). Because colonies of *R. marginata* are perennial, they often outlive their queens, providing opportunities for some of the workers to become queens. Such *Serial Polygyny* results in the simultaneous presence of different matrilines in a colony (Fig.5) (Gadagkar *et al.*, 1990a). Electrophoretic and pedigree analysis show that polyandry and serial polygyny together result in a sufficient decrease in the genetic relatedness between workers and brood so that the advantage of haplodiploidy for the evolution of sociality postulated by Hamilton is largely forfeited in this species.

PRE-IMAGINAL CASTE BIAS

Alexander (1974) proposed the theory of *Parental Manipulation* according to which some individuals end up as sterile workers because they are manipulated by their parents at a stage in their life when they are helpless. A similar idea was embodied in the *Sub-Fertility Hypothesis* of West-Eberhard (1975), who argued that sub-fertile individuals, produced by whatever mechanism should be selected more easily to become workers.

To test if there is variation in fertility as predicted by these hypotheses, we isolated a large number of female *R. marginata* at eclosion and tested them for their ability to start new nests and lay eggs. The results of such an experiment showed that only about half the eclosing females are capable of doing so (Gadagkar *et al.*, 1988; Gadagkar *et al.*, 1990b). Clearly, the other half are relatively sub-fertile. In a more recent experiment we found that nests in which larvae are fed at a relatively higher rate produce a relatively greater proportion of females that can initiate nests on their own (Gadagkar *et al.*, 1991). Thus caste is not determined entirely in the adult stage; there is some pre-imaginal biasing of caste so that all

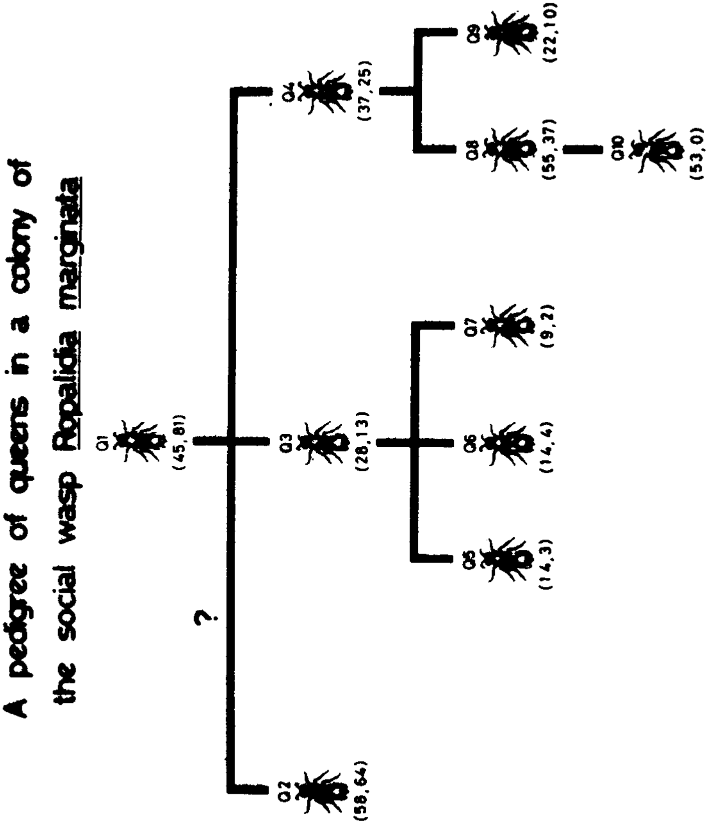

Figure 5. A pedigree of queens seen on a nest of *Ropalidia marginata*. There are ten queens labelled Q1 to Q10. There was only one queen at any given time but queens succeeded each other according to the serial number Q1, Q2 etc. Notice that the relationship between Q2 and Q1 is unknown but all other relationships are known. Thus new queens were either sisters (e.g. Q4 was a sister of Q3), Nieces (e.g. Q10 was a niece of Q9), cousins (e.g. Q8 was a cousin of Q7) or daughters (this situation was seen in other colonies) of their immediate predecessors queens.

females are not born equally fertile. This is evidence in support of the mainpulation and sub-fertility hypotheses but it is only partial evidence. In natural colonies most individuals are workers and only a small number become queens whereas in our experiments about 50% of the individuals were capable of reproducing. The question remains therefore as to why only a small proportion of these 50% become queens in nature.

MUTUALISM

Lin and Michener (1972) put together a variety of data to show that in many insect societies complete sterility and altruism are lacking. They argued therefore that insect societies may often originate due to the possibility of mutual benefit to all the members of the group. The failure of the genetic hypothesis and the limited success of the manipulation and subfertility hypotheses in explaining the presence of a sterile worker caste in *R. marginata* persuaded me to take a fresh look at the idea of Mutualism. The proposal that mutualism could have an important role in the evolution of insect societies has not often been taken seriously because of the impression that mutualism, by definition, cannot give rise to sterile worker castes. This objection may however, be overcome by imagining that wasps may be programmed not to be sterile or fertile but to choose between solitary and group life. If the roles of queen and worker in the group mode are now decided by chance factors, then it is possible that individuals who are programmed to "gamble" and join a group will do better, on the average, compared to those who shy away from the risk of group life and remain solitary (Gadagkar 1990b; 1991a).

The fact that colonies of *Ropalidia* consist of several individuals who are capable of reproducing and that workers quite often succeed in driving away the queens of their colony and taking over the role of the queen lends credence to this *gambling hypothesis*; females who stay back and work are not doomed to be sterile - some of them at least can become queens and inherit the whole colony which may be much more profitable than trying to start a new single foundress nest.

THE ROLE OF DEMOGRAPHY

The role of demographic factors in promoting the evolution of insect societies has so far been relatively unexplored. I have therefore recently constructed a hierarchy of models to illustrate, within the framework of inclusive fitness theory, that demographic factors can select for a worker caste in social insects (Gadagkar 1990c; 1991b). The first model in the series shows that *Delayed attainment of reproductive maturity* lowers the inclusive fitness of a solitary foundress relative to that of workers. The second model shows that *Variation in age at reproductive maturity* makes the worker strategy more profitable to some individuals than to others and thus predicts the coexistence of single-foundress and multiple-foundress nests. The third model demonstrates the probability of *Mixed reproductive strategies* so that, some individuals whose attainment of reproductive maturity is expected to be delayed can first act as workers and later switch over to the role of a queen or nest foundress. The fourth model shows that identical adult mortality rates can have different consequences for workers and solitary nest foundresses. This is because a solitary foundress will have to necessarily survive for the entire duration of development of her brood while a worker can hope to get proportional fitness returns for short periods of work. Workers may therefore be said to have *Assured fitness returns.*

In combination with assured fitness returns, delayed reproduction and variation in age at reproductive maturity become more powerful in selecting for worker behaviour and mixed reproductive strategies become available to a wider range of individuals. These theoretical models have been tested using field and laboratory demographic data on *R. marginata* and demonstrate that such factors provide a consistently more powerful selective advantage for the worker strategy than genetic asymmetries created by haplodiploidy.

THE ROUTE TO SOCIALITY

Based on our studies on *Ropalidia* in India and a review of the literature on other social insects, I have hypothesised a route to social evolution which has three stages (Gadagkar 1990b; 1991a). In the *Gambling stage,* individuals come together for mutual benefit and egg laying opportunities are decided by chance factors. When group life becomes possible by this method, some individuals may learn to cheat and increase their chances of reproduction by manipulating others. From this *Manipulation Stage,* they may either revert to solitary life or may enter the *Recognition Stage.* In this final stage, the losers in the gamble learn to distinguish close genetic relatives from distant ones (for e.g., among the different patrilines and matrilines in the colony) and thus compensate for the loss in fitness suffered due to having been manipulated. Demographic factors such as those described above can facilitate social evolution at each stage although they are likely to have been more important in the early stages.

I believe that a combination of empirical and theoretical investigations on a model system such as *R. marginata,* as illustrated here, can throw considerable light on the forces responsible for the evolution of altruism in insects.

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