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SOCIAL BIOLOGY OF *ROPALIDIA* : INVESTIGATIONS INTO THE ORIGINS OF EUSOCIALITY

RAGHAVENDRA GADAGKAR

Centre for Ecological Sciences and Centre for Theoretical Studies,
Indian Institute of Science, Bangalore-560 012, INDIA.

The evolution of sterile worker castes found in most social insects presents an obvious challenge to Darwin's theory of natural selection. Highly eusocial insects such as ants and honeybees have morphologically differentiated worker and reproductive castes and may be studied with the aim of understanding how eusociality is maintained by natural selection or why highly eusocial species do not revert to the solitary state. In primitively eusocial species such as many kinds of bees and wasps reproductive and worker castes are morphologically identical and social roles are left flexible to be decided by social interactions amongst the adults. Such species may therefore be studied with the hope of understanding the forces that promote the origin of eusociality. Independent founding species of the tropical wasp genus *Ropalidia* provide exceptionally good model systems for such investigations. Female wasps eclosing on nests of *R.marginata* and *R.cyathiformis* have the option of leaving their natal nests to found their own single foundress nests or remaining on their natal nests to assume the role of a worker. The question then is, why such a large number of females remain on their natal nests after eclosion?

At the time we began our investigations, three classes of theories namely Kin selection (or Haplodiploidy hypothesis) (1), Parental manipulation (2) or Subfertility hypothesis (3) and Mutualism (4) were widely known to provide potential answers to this question. The measurement of sex-investment ratios and of the productivities of single - and multiple-foundress nests were the two methods that were then being used in attempts to distinguish between these potential theories. The few attempts that had been made in this direction had not been very successful (5). Besides, these methods seemed inappropriate for species such as *R.marginata* and *R.cyathiformis* because neither sex investment ratios nor differential productivities can be measured accurately in these species. This is because all females cannot be unambiguously classified into workers and reproductives; any female has a certain probability of becoming either a worker or a queen. For this reason, it became necessary to develop alternate methods to distinguish between the competing theories. The method I have used is primarily based on quantitative ethology. Constructing time activity budgets for individually identified members of several colonies and subjecting them to multivariate analysis revealed a behavioural caste differentiation into Sitters,

Fighters and Foragers (6). Although the foragers seem to have little or no chance of future reproduction, both Sitters and Fighters appear to keep their option for direct reproduction open while contributing towards the welfare of the colony. Social organisation based on such behavioural caste differentiation rather than one based on a rigid dominance hierarchy led by a despotic queen, suppressing all her nestmates into worker roles (7), prepared the stage for our enthusiasm for mutualistic models for the origin of eusociality. The complex behaviour of the wasps including the ability of some individuals to leave their natal nests along with a few workers and establish themselves as queens of new colonies and the ability of wasps within a colony to behave as two coordinated groups (8) removed any doubt about the ability of the wasps to adopt complex strategies that may be required for social evolution through mutualism.

At the same time we have accumulated evidence against the haplodiploidy hypothesis. We have established that queens of *R. marginata* mate multiply, use sperm simultaneously from different males and thus break down the genetic asymmetries created by haplodiploidy (9). Frequent queen replacements further reduce worker-brood genetic relatedness. Indeed, we have evidence that workers often rear complex mixtures of full-siblings, half-siblings, nieces, nephews and cousins (10). This may not be a serious problem for kin selection if workers can discriminate different levels of genetic relatedness within the colony and give preferential aid to close relatives (11). We therefore set up experiments to test this possibility. The results of these experiments suggest that labels and templates used in kin recognition are acquired by the wasps from such common sources outside their bodies, as, their nest or nestmates. This makes it unlikely that genetic heterogeneity within a colony will be recognised and used in dispensing altruism (12). In addition, these experiments showed that factors other than genetic relatedness modulate tolerance and acceptance of foreign conspecifics. Even genetically unrelated individuals sometimes cooperate in the founding of new colonies (13). These findings, while suggesting an insignificant role for haplodiploidy further strengthened our faith in mutualistic theories.

The ideas of parental manipulation and subfertility have been poorly tested. We therefore set up experiments to test the hypothesis that all eclosing females are potentially capable of becoming egg-layers. It turns out that about 50% of eclosing females do not initiate nests and lay eggs even if rescued from any inhibition by conspecifics. The queen and other adults in a colony appear to influence the future caste of the brood by channelling them either into a developmental pathway leading to adults programmed to be good eaters and good egg-layers or into an alternate pathway leading to poor eaters and poor egg-layers (14). However, the extent of such pre-imaginal caste bias is obviously insufficient to explain the fact that most individuals become workers and only a few become queens.

The clear choice before us was therefore mutualism. But, mutualistic models have not been taken seriously because they are expected to fall short of giving rise to sterile castes. The

"Gambling" hypothesis is one way out of this difficulty. The advantages of group living may be so great that even if the roles of egg-layer and sterile worker are decided by chance, an average member of a group may do better than a solitary individual. Thus the hypothetical "Gambling" allele which programmes its bearers to take the risk of being part of a group may spread in the population at the cost of the wild type allele which programmes its bearer to be risk-averse and remain solitary. If fertility or sterility are thus the result of phenotypic plasticity, we may see a fraction of sterile individuals in every generation although there is no allele for sterility (15)! The perennial colony cycle of *R.marginata* with its frequent queen replacements is undoubtedly responsible for providing wasps, that stay back on their natal nests, a finite chance of direct reproduction. The answer to our original question then would be that most individuals stay back on their natal nests because of some hope of direct reproduction. Those that realize such hope must compensate in some measure for the remaining that die as workers (10).

These investigations and a survey of the literature on other kinds of social insects suggests a route to eusociality that has three stages: the "Gambling" stage where group living is brought about due to the advantages of mutualistic interactions followed by the "Manipulation" stage where parental manipulation and subfertility begin to act and finally the "Recognition" stage where genetic asymmetries created by haplodiploidy may be recognised and the species may be locked into the highly eusocial state. The time has come, however, when we should be looking beyond the three theories that we began with. Towards this goal, our recent modelling efforts have shown that additional factors such as "Assured fitness returns", "Delayed reproduction" and "Variation in age at reproductive maturity" may all act to select for worker behaviour in such species as *R.marginata* (unpublished).

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