

Scientific Contributions of Prof. Raghavendra Gadagkar

Raghavendra Gadagkar has established an active research programme in insect sociobiology, at the Centre for Ecological Sciences, Indian Institute of Science, Bangalore, India. His work has contributed significantly to our understanding of the structure and evolution of insect societies and has considerably altered our view of the forces that mould the evolution of social life in animals. After obtaining a PhD in molecular biology, Gadagkar made what was then an unusual twist in his career and turned his attention to the study of social insects. The unique perspective that this has permitted him to bring to the study of social evolution has proved significant.

In an attempt to provide the beginnings of a solution to the apparent paradox of altruism shown by members of insect societies, Gadagkar has chosen the locally available Indian species of primitively eusocial wasp *Ropalidia marginata*, scientifically unknown and belonging to a poorly studied genus, but uniquely suited for his purpose. Exploiting the fact that long-term studies on a tropical species has the potential to provide new insights, Gadagkar and his team of students have relentlessly pursued empirical and theoretical, field and laboratory work on this single species for over 35 years to considerably alter our understanding of the early stages of the evolution of insect sociality. Perhaps Gadagkar's most significant contribution has been the use of a variety of approaches to demonstrate the inadequacy of focusing exclusively on the role of genetic relatedness in driving social evolution. These include the use of biochemical techniques to show that queens mate multiply and mix sperm from different males, the construction of the first ever pedigrees for social insect queens to show that workers rear rather distantly related brood, the experimental demonstration that workers are unlikely to discriminate between different classes of relatives within their colony and the first clear demonstration that all individuals are not equally fit for social or solitary life. Having done that, Gadagkar has developed a new class of theories, the focus of which is demography, a factor previously unexplored in this context. His *Assured Fitness Returns* model is a simple and elegant example of how group living can confer advantages over solitary life that are independent of genetic relatedness between the donor and recipient of altruism. Put in another way, Gadagkar's work has pointed out that the cost and benefit terms in Hamilton's rule may be more important than the relatedness term.

Gadagkar has not restricted his attention to evolutionary questions alone. He has pursued in parallel, an equally rigorous and original programme of experimental and

theoretical work focusing on proximate questions of social organization and queen-worker interaction. Using multivariate statistical analysis of time-budgets of individually marked wasps in a uniquely original way, he discovered behavioural caste differentiation in this species that lacks morphological castes. Gadagkar discovered pre-imaginal caste bias in this primitively eusocial species and demonstrated larval nutrition as its basis, another first for primitively eusocial insects. These findings have important implications for our understanding of the evolution of sociality. Pursuing the idea that *R.marginata* may be more socially advanced than a typical primitively eusocial species, Gadagkar and his students looked for and found, a remarkably well-developed, honey bee like age polyethism and developed a computer simulation model to show how a dynamic interplay between a pair of hypothetical activator and inhibitor substances can generate a flexible, self-regulating age polyethism among interacting individuals.

Even more unexpectedly for a primitively eusocial species, Gadagkar and his students have demonstrated that queens of *R.marginata* are behaviourally subordinate, meek sitters. This raises questions regarding how such queens become queens in the first place, how they inhibit worker reproduction and how they regulate non-reproductive activities of their workers. Attempts to answer these questions have begun to suggest that *R.marginata* queens start their careers as aggressive queens and probably switch to pheromonal control of worker reproduction, which is why they can afford to be behaviourally meek sitters. As a response to this behaviour on the part of their queens, the workers have responded by self-organizing their own non-reproductive activities and thereby gaining indirect fitness without much prodding by the queen.

Another remarkable feature of *Ropalidia marginata* society that Gadagkar and his students have discovered concerns the smooth and conflict-free succession that happens from one queen to the next. Through a series of cleverly designed experiments, Gadagkar and his students have demonstrated that even though human observers cannot predict the identity of the successor, the wasps themselves appear to know who the successor would be in the event of the death or loss of the queen. Indeed they have demonstrated that there is a long reproductive queue of cryptic successors with designated positions in the queue.

While conducting these researches Gadagkar has been exceptionally active in communicating his findings to specialist and general audiences. In addition to 270 publications which include refereed papers, conference proceedings, general articles and book reviews, he has authored two books, both published by Harvard university Press, USA. The first, entitled *Survival Strategies*, is a very successful exposition of the field of

behavioural ecology and sociobiology to a general audience and has already been translated into Chinese and Korean and is used as a text/ancillary text in some universities in India and USA. The second, entitled *The Social Biology of Ropalidia marginata*, is a more technical summary of over 20 years of research by Gadagkar and his students.

From time to time, Gadagkar has also turned his attention beyond *Ropalidia*. His paper with John Bonner translating insights from social evolution in wasps to social evolution in soil amoebae, and his theoretical paper on the evolution of caste polymorphism by *genetic release followed by diversifying evolution* and his review of the then existing literature on the peacock undertaken to exhort Indian biologists to take up evolutionary studies, are just some examples.

As the founder chair of the Centre for Contemporary Studies at IISc, Bangalore, Gadagkar has initiated a new experiment that endeavours to engage some of the best practitioners of different disciplines in the human sciences, such as philosophy, sociology, economics, law, literature, poetry, art, music, cinema etc. and aims to forge meaningful interaction between the natural and human sciences with special focus on exposing graduate students to the diverse research methodologies of different disciplines and thus creating opportunities for them to rethink the foundations of their own disciplines.

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