



PLATINUM JUBILEE

of the

INDIAN NATIONAL SCIENCE ACADEMY

10th-12th January, 2009

Proceedings of the Inauguration



IN PRAISE OF ORGANISMAL BIOLOGY

Professor Raghavendra Gadagkar

I have been asked to describe my efforts in the past 25 years or so, to remain at the cutting edge of international scientific research. I do so with a certain degree of hesitation and at the risk of sounding pompous. I am a biologist and biology today is an incredibly rich and complex discipline. Hence biology can be practiced in many different ways. An additional reason for this is that life processes are organized in many different hierarchical levels. At one level you have ecosystems, forests, populations and then the individual organism, which can be studied in its own right. At the other extreme, if you go deep inside an individual, you have cells, tissues, organs, organelles and finally, molecules. The manner of doing biology at these different levels of organization

can be so different that they can be mutually incompatible and often mutually incomprehensible. While it is obvious that studying life processes at all possible levels of organization is necessary and interesting, this needs different classes of biologists trained in rather different methodologies, and driven by quite different philosophical orientations. All this makes it almost impossible to maintain a reasonable balance between the different kinds of biology. This is true at the national and even international level, not to speak of the impossibility of maintaining a balance within an institution or department of biology.

For the purpose of this talk I will broadly classify biology into sub-organismal biology which includes cellular and molecular



biology, and organismal biology which includes population biology, behaviour, ecology and evolutionary biology. Evolution should of course cut across these barriers but even today evolution is more often practiced as a discipline among organismal biologists than among cell and molecular biologists, but this situation is gradually changing. Once dichotomized in this way, we find a major practical difference in pursuing sub-organismal and organismal biology. Practicing cell and molecular

GADAGKAR, Raghavendra (b. 28 June 1953 in Kanpur), obtained Ph.D. (1979) in Molecular Biology from the Indian Institute of Science, Bangalore and joined as Research Associate at the Centre for Theoretical Studies, and became Professor in (1997-), at the Centre for Ecological Sciences.

Professor Gadagkar's major research interests are behaviour, ecology and evolution. Gadagkar teaches courses in general biology, animal behaviour, behavioural ecology and sociobiology and statistics. The origin and evolution of cooperation in animals, especially, in social insects, such as ants, bees and wasps, is a major goal of his research. By identifying and utilizing crucial elements in India's biodiversity, he has added a special Indian touch to his research. He has published over 200 research papers and two books entitled *Survival Strategies* (Harvard University Press, USA 1997 and Universities Press, Hyderabad, 1998, since translated into Chinese and Korean) and *The Social Biology of Ropalidia marginata* (Harvard University Press, USA, 2001), which summarizes over twenty years of his research aimed at understanding the evolution of eusociality. He served as Chairman, Centre for Ecological Sciences (1992-2002) and is the Founding Chairman of the Centre for Contemporary Studies (2004-).

He is a Fellow of all three Science Academies, i.e., Indian National Science Academy, India Academy of Sciences, National Academy of Sciences, India and Third World Academy of Science and Foreign Associate of the National Academy of Sciences, USA.

Gadagkar is the recipient of a number of awards including Shanti Swarup Bhatnagar Prize, BM Birla Science Prize, Homi Bhabha Fellowship, BP Pal National Environment Fellowship on Biodiversity, and the Third World Academy of Sciences Award in Biology.

Present Address: Professor and JC Bose National Fellow, Centre for Ecological Sciences, Indian Institute of Science, Bangalore-560012.

biology almost always requires significant technological augmentation of our own sensory capabilities – we need fine chemicals and instruments to isolate the components we wish to study, centrifuges, chromatographs and the like for their separation and microscopes, spectrometers and the like to visualize them. This inevitably makes the pursuance of sub-organismal biology a technology intensive and financially expensive proposition, leaving little scope for the amateur or laymen to participate. Relatively speaking, organismal biology deals with structures and phenomena that are in the perception range of our own sensory capabilities. There is a great deal we can do without special isolation, separation and visualization, and without the need for sophisticated technology and large research grants, indeed often without the need for laboratory experimentation, leaving ample scope for laymen and amateurs to make significant contributions – just think of the life time's work of Charles Darwin. There are two more features of organismal biology that I am yet to mention. These are that it is facilitated by access to a rich biodiversity and is very labour intensive. The things that organismal biology is independent of (technology, fine chemicals, money) and those that it is dependent on (biodiversity, manpower) together make it just the right choice for someone like me in a developing country, in my attempt to stay at the cutting edge of international science. This is a necessary and sufficient explanation for why I am an organismal biologist.

Perhaps the most significant remaining challenge in the area of evolutionary organismal biology is the evolution of sociality and its associated altruism. Consider a honey bee colony

familiar to most of us. Honey bees live in populous colonies consisting of tens of thousands of individuals. Each colony consists of a single fertile female bee which is referred to as the queen. The rest of the female members of the colony are small, nearly sterile worker bees. And then there are a small numbers (usually in the hundreds) of male bees referred to as drones. Virgin queens begin their adult life by embarking on a nuptial flight, mate with a dozen or more drones from unrelated colonies, gather and store a large supply of sperm in their spermathecae, return to the nest of their birth and settle down to a life time of egg laying. The only other thing they do is to produce a large number of different kinds of pheromones that regulate the functioning of the colony. The legendarily lazy drones leave their nest of birth in an attempt to mate with virgin queens from alien colonies and die in the act of mating.

All the labour that is required to make the society function, such as cleaning the nest, building and repairing the nest, nursing the larvae, unloading and processing food brought by the foragers, guarding the nest and leaving the nest to bring back pollen

and nectar, is all performed by the worker bees. Workers are incapable of mating and although they can lay a small number of unfertilized eggs, they almost never do so in the presence of the queen. Thus most workers spend their whole lives working for the welfare of the colony and to enable the queen to reproduce, while they themselves die without leaving behind any offspring. In terms of their Darwinian fitness this is equivalent to suicide. Indeed when their nests are marauded by predators they commit what may be even more easily termed as suicide – they fly out and sting the offending object in a process which results in their death within a few minutes. This is because their stings are armed with barbs pointing outwards making it impossible for them to withdraw the sting once inserted. When they do fly away, their abdomens rupture and they leave their sting, the poison gland and parts of their intestines hanging on their victims. It turns out that the poison gland continues to



pump venom into the body of the victim for several seconds. This makes the worker bee a very effective venom delivery apparatus although she herself dies in the process. Whether it is the practice of life-time sterility in the service of another individual's reproduction or suicide to facilitate another individual's survival and well being, the net result is the same – loss of Darwinian fitness.

How does natural selection promote the evolution and maintenance of such altruistic traits? Why does selection not eliminate altruists and promote selfish behaviour resulting, if so be it, in a solitary mode of life for all animals. Similar acts of altruism, to a lesser or greater degree but always posing a challenge to classical Darwinian theory, are encountered quite frequently in the living world. WD Hamilton paved the way to a possible solution of this paradox by proposing what has now come to be known as kin

selection. Put simply, Hamilton put forward the idea that an altruistic trait would indeed be favoured by natural selection if the cost of the altruism to the actor, is less than the benefit to the recipient devalued by the proportion of genes shared between the altruist and the recipient. This is often referred to as Hamilton's rule (Gadagkar 1997).

This was an elegant theory and proved to be mathematically robust. But what good is a theory if it cannot be empirically verified. In other words we need to show that animals behave as if they obey Hamilton's rule. This is often the hard part because unlike the theory itself which can often dawn upon you with a flash of brilliance, empirical testing is a long, arduous and messy affair. The brilliance of the theory and our frustration due to the inability to get clinching empirical confirmation characterized the

Although there is a single queen per nest she is not morphologically differentiated from the workers. Indeed most workers are potentially capable of becoming queens and some do so by ousting aging queens. Besides, the wasps are also capable of leaving the nests of their birth and leading an essentially solitary life.

field when I began. Fresh with a PhD in molecular biology and with a clear decision to switch to organismal biology rationalized by my decision to stay and work in India rather than emigrate to the west, I decided to take up the challenge. The first decision I made was to choose a brand new and locally available model organism. I was fortunate in choosing the tropical, primitively eusocial polistine wasp *Ropalidia marginata*. This has proved to be my most important ally in attacking the paradox of altruism. *R. marginata* builds small open, paper carton nests which often contain no more than 20 or 30 wasps, all of which can be relatively easily marked individually and observed throughout their life span, usually of a few weeks. More importantly, although there is a single queen per nest she is not morphologically differentiated from the workers. Indeed most workers are potentially capable of becoming queens and some do so by ousting aging queens. Besides, the wasps are also capable of leaving the nests of their birth and leading an essentially solitary life, each solitary nest foundress building a nest all by herself and raising her brood to adulthood unaided by any other wasp. In other words these wasps appear to be on the brink of sociality as they are capable of both selfish, solitary behaviour as well as altruistic, social behaviour.

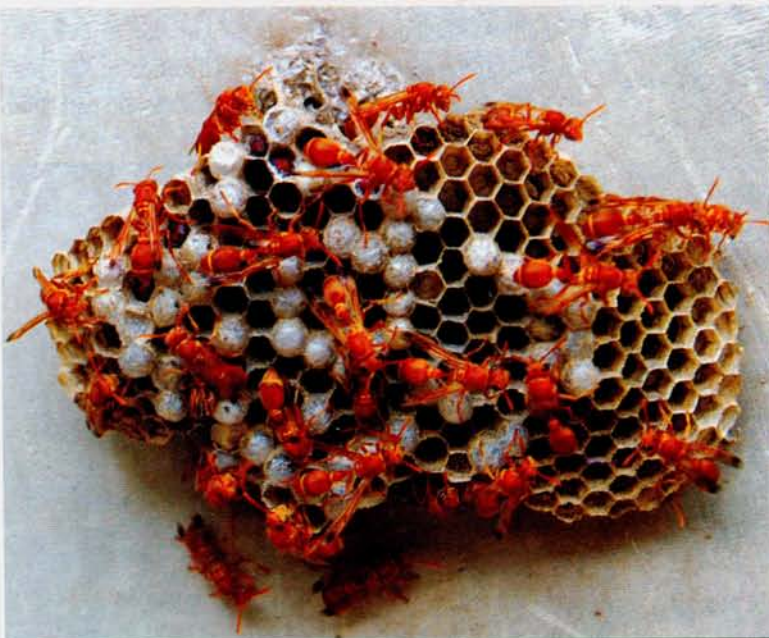


Figure 1. A typical nest of the primitively eusocial wasp *Ropalidia marginata* (Photo: Thresiamma Varghese)

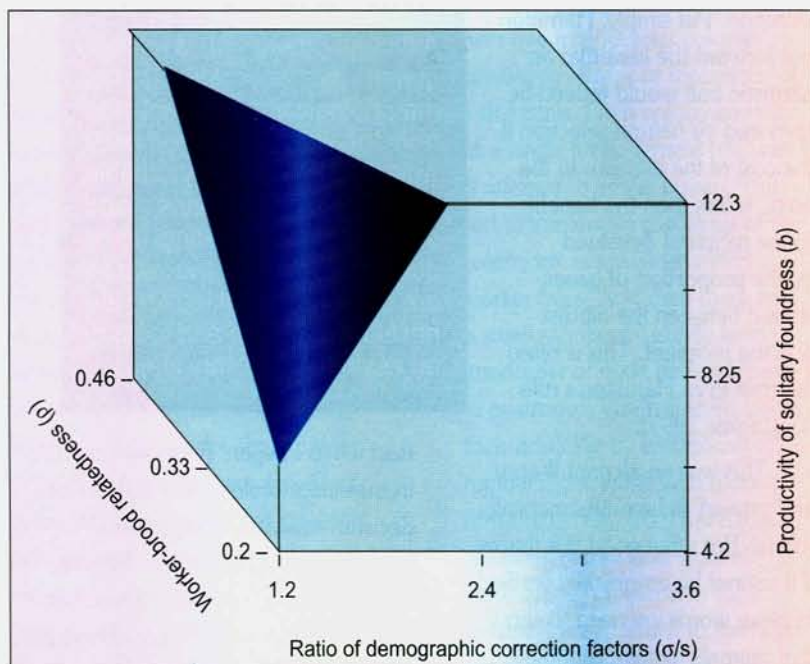


Figure 2. A graphic illustration of the unified model showing the parameter space where worker behaviour is selected (unshaded 94.9%) and the missing chip of the block where solitary nesting behaviour is favoured (for details see Gadagkar 2001). (Reprinted with permission from Harvard University Press, Copyright 2001)

Hence it is reasonable to ask why altruistic wasps do not behave selfishly, as most wasps appear to be capable of following both selfish and altruistic life styles.

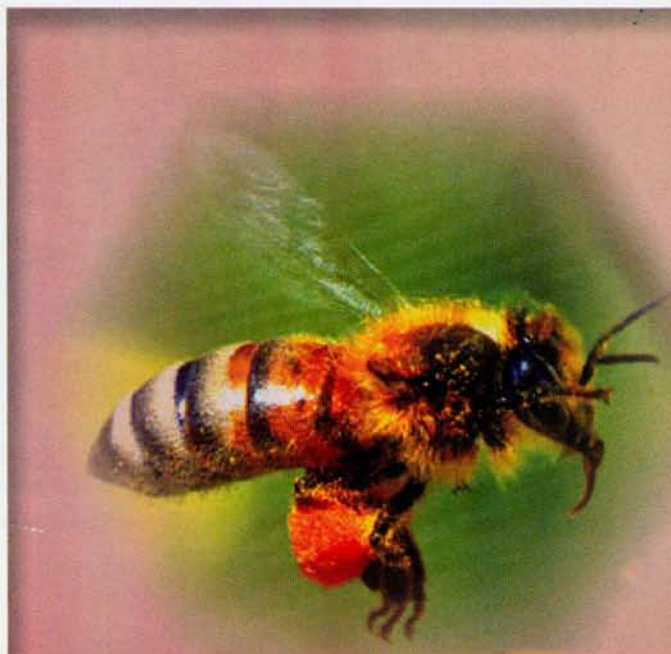
My second decision was to deliberately stay off the beaten track. Most people investigating these phenomena were rather obsessed with the potential explanatory power of genetic relatedness and with the new molecular techniques of measuring genetic relatedness. Thus many investigators completely ignored the cost and benefit terms in Hamilton's rule and focused exclusively on the relatedness term. It was obvious to me that no complete confirmation or refutation of the theory would be possible without simultaneously measuring all three terms – cost, benefit and relatedness. My decision to focus on the cost and benefit terms, in addition to the relatedness term was very much in tune with the description of organismal biology I have given above. Measuring the cost and benefit terms requires rather little sophisticated technology, instrumentation and money but requires a great deal of patient hard work in the field and a large manpower – just right for India.

It is perhaps fair to say that I also brought at least one new idea to the field, which facilitated my staying at the cutting edge. I discovered a novel phenomenon, quite independent of genetic relatedness which can

potentially promote the evolution of group living and its associated altruistic behaviour. The idea is a rather simple one and I called it Assured Fitness Returns. A solitary wasp has to necessarily survive until she brings up her offspring to adulthood. If she dies in the midst of this effort she will lose all her investment up to the time of her death. In other words a solitary foundress has relatively little assured returns for her investment. If mortality rates are high and brood development is long, solitary foundresses will have relatively low fitness. Workers in multi-female nests on the other hand have relatively higher assured fitness for their investment. Even if a particular worker were to die after raising

brood up to a point, she will not lose all her investment as other workers can continue her work and eventually bring those items of brood to adulthood. Even when mortality is high and brood development is long, altruistic workers will have relatively higher fitness.

My choice of an excellent model system, my decision to deviate from the beaten track and pay attention to all the three terms in Hamilton's rule and my lucky break in coming up with the idea of Assured Fitness Returns were all necessary but hardly sufficient.



The wasps appear to be on the brink of sociality as they are capable of both selfish, solitary behaviour as well as altruistic, social behaviour. Hence it is reasonable to ask why altruistic wasps do not behave selfishly, as most wasps appear to be capable of following both selfish and altruistic life styles.

To produce cutting edge research, what was needed in addition was of course a great deal of hard work by a very large number of committed students over many years. And this was much easier to obtain than it almost certainly would have been to obtain state-of-the-art technology, vast sums of money and a sophisticated laboratory. Over the years we have succeeded in demonstrating that Assured Fitness Returns does indeed provide a powerful new explanation for the evolution of altruism. In *R. marginata* Assured Fitness Returns makes the altruistic worker strategy 3.6 times more advantageous than the selfish solitary foundress strategy and 2.4 times more powerful than the then prevailing Hamilton's model based on Haplodiploidy (Gadagkar 1990, 1991). Combining more theory and much empirical field and (some) laboratory work, we also succeeded in devising ways and means of measuring (or at least comparing) the cost, benefit and relatedness terms of workers and solitary foundresses. The net result was a unified model for the evolution of eusociality in *R. marginata*, which predicted that altruistic worker behaviour should be selected in about 94.9% of the parameter space and selfish solitary behaviour in only 5.1% of the parameter space. But here again is a theoretical

prediction that needs empirical confirmation – after all theory and experiment should follow each other in an endless cycle. Along came another student who performed painstaking field work to show that in nature 92.5-95.4% of *R. marginata* wasps prefer to nest in groups (altruistic worker strategy) and only 4.6-7.5% prefer to nest solitarily (selfish strategy), thus providing striking confirmation of the theoretical prediction (Shakarad and Gadagkar 1995). In a recent monograph on *The Evolution of Social Wasps*, James Hunt described our work as “...the only study of social wasps that has quantified all three variables of Hamilton's rule” and remarked that “No other study of social insects approaches the level of detail that Gadagkar and his group achieved” (Hunt 2007).

I have only had time to describe one example of cutting edge research we have been able to perform using *R. marginata* but in fact this promises to be a ceaseless activity (Gadagkar 2001, 2009). And of course I and my students have no monopoly over organismal biology. The main motivation for describing these success stories is to point out the great advantage of organismal biology for colleagues in developing countries such as ours.

Acknowledgements

The work I have described in this essay was done over a 25 year period and was only possible due to the friendship, collaboration and shared passion for organismal biology of a large number of students and colleagues. This research has been supported by the Centre for Ecological Sciences, Indian Institute of Science, Jawaharlal Nehru Centre for Advanced Scientific Research, Bangalore, Indian National Science Academy, Delhi and by several agencies of the Government of India including the Department of Science and Technology, Department of Biotechnology, Ministry of Environment and Forests, Council of Scientific and Industrial Research.

References

1. Gadagkar R, 1990. Evolution of eusociality: the advantage of assured fitness returns. *Phil. Trans. Roy. Soc. Lond.* **B329**: 17-25.
2. Gadagkar R., 1991. Demographic predisposition to the evolution of eusociality: a hierarchy of models. *Proc. Natl. Acad. Sci. USA.* **88**: 10993-10997.
3. Gadagkar R, 1997. *Survival Strategies: Cooperation and Conflict in Animal Societies*. Cambridge, Mass.: Harvard University Press and Hyderabad, India: Universities Press.
4. Gadagkar R, 2001. *The social Biology of Ropalidia marginata: toward understanding the evolution of eusociality*. Cambridge, Mass.: Harvard University Press.
5. Hunt JH, 2007. *The Evolution of Social Wasps*. New York, USA: Oxford University Press.
6. Shakarad M and Gadagkar R, 1995. Colony founding in the primitively eusocial wasp, *Ropalidia marginata* (Lep.) (Hymenoptera: Vespidae). *Ecol. Entomol.* **20**: 273-282.